

On some new Phelliinæ from New Guinea.

By

Gilbert C. Bourne, M.A., D.Sc., F.R.S.,

Fellow of Merton College, Oxford, and Linacre Professor of Zoology
and Comparative Anatomy.

With Plates 3-5, and 2 Text-figures.

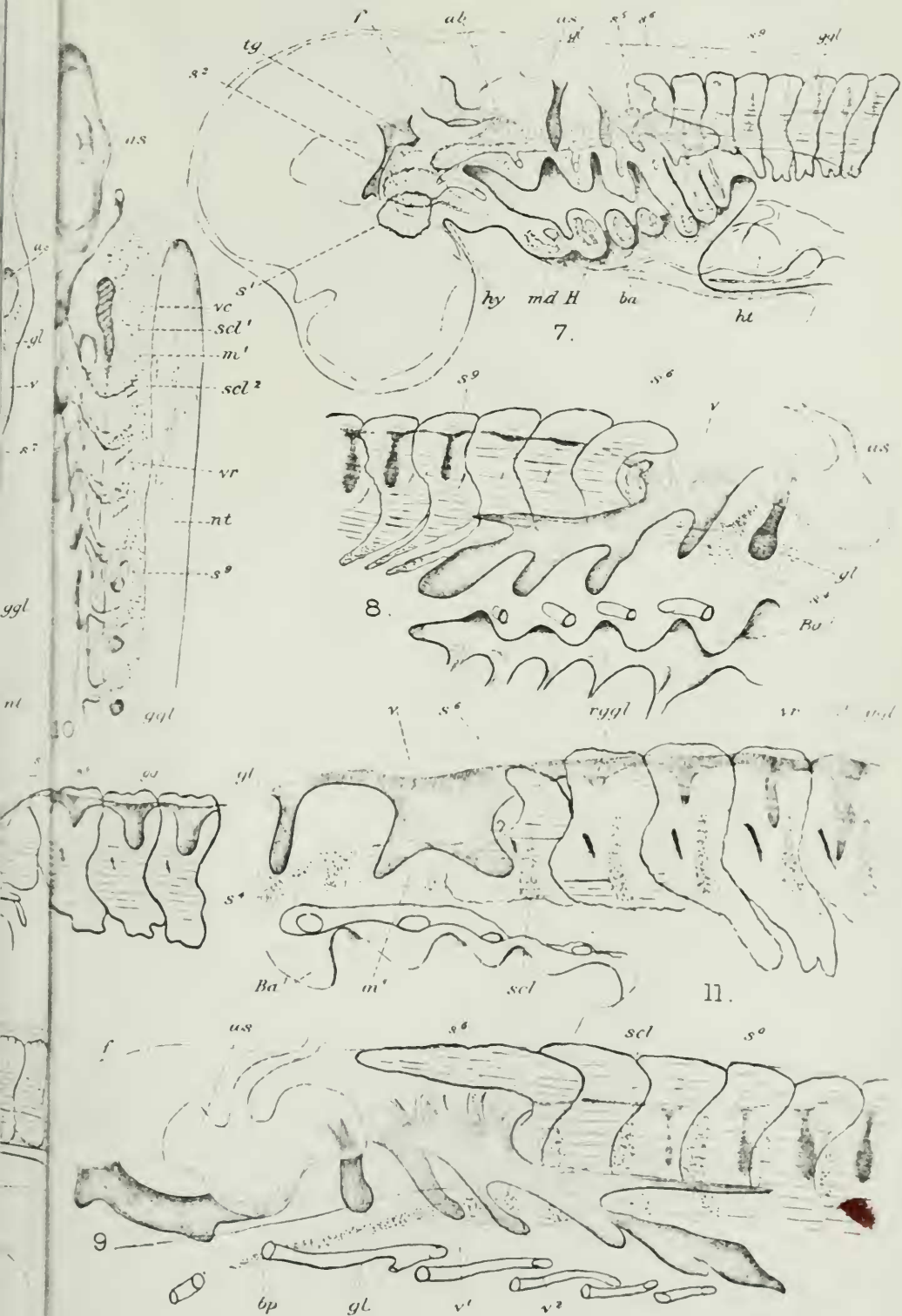
THE genus *Phellia*, instituted by Gosse (14) and placed in the family Sagartiadæ, was originally defined by him as follows: "Base adhering to rocks; little exceeding the column. Column pillar-like in expansion; the margin tentaculate, without parapet or fosse. Surface smooth, pierced with loop-holes; partly clotted with a tough epidermis, which is rough externally, firmly adherent to the skin. Disc concave; the edge not undulate. Tentacles few, in more than one row; barred. Mouth not raised on a cone; lip thickened. Acontia discharged but reluctantly."

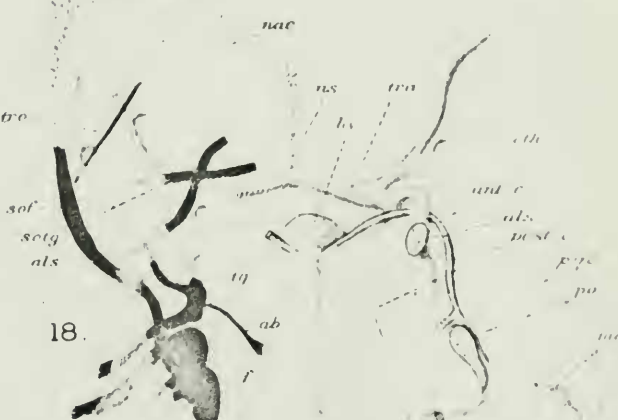
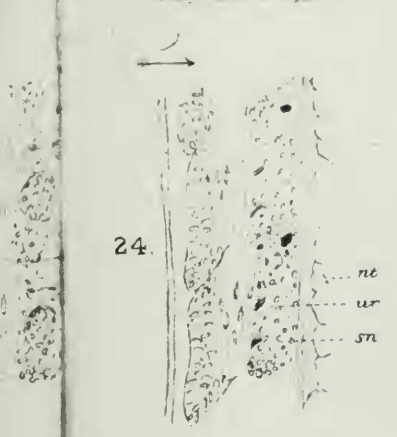
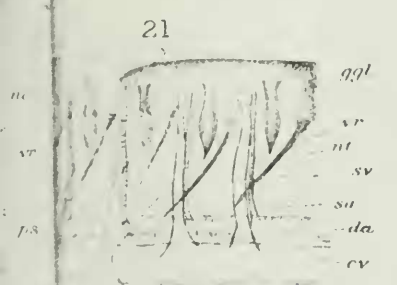
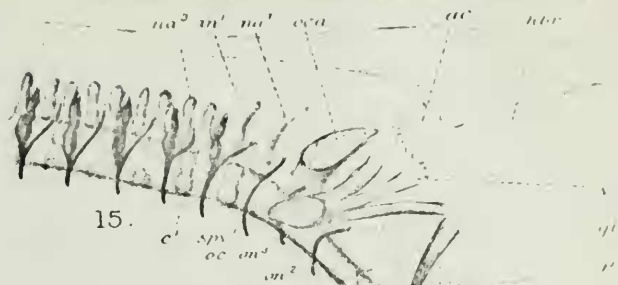
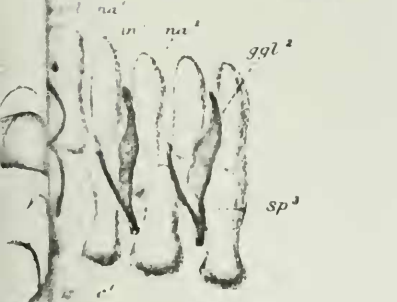
The type species is *Phellia mureocincta*, Gosse, and to this the author of the 'Actinologia Britannica' added *gausapata* and *picata*, and included the genus in his family Sagartiadæ, one of the characters of which, as given by Gosse, was "integument pierced with loop-holes (cinclides) —special orifices, through which are emitted and retracted fleshy cords (acontia) which have their origin in the membranous partitions of the body-cavity."

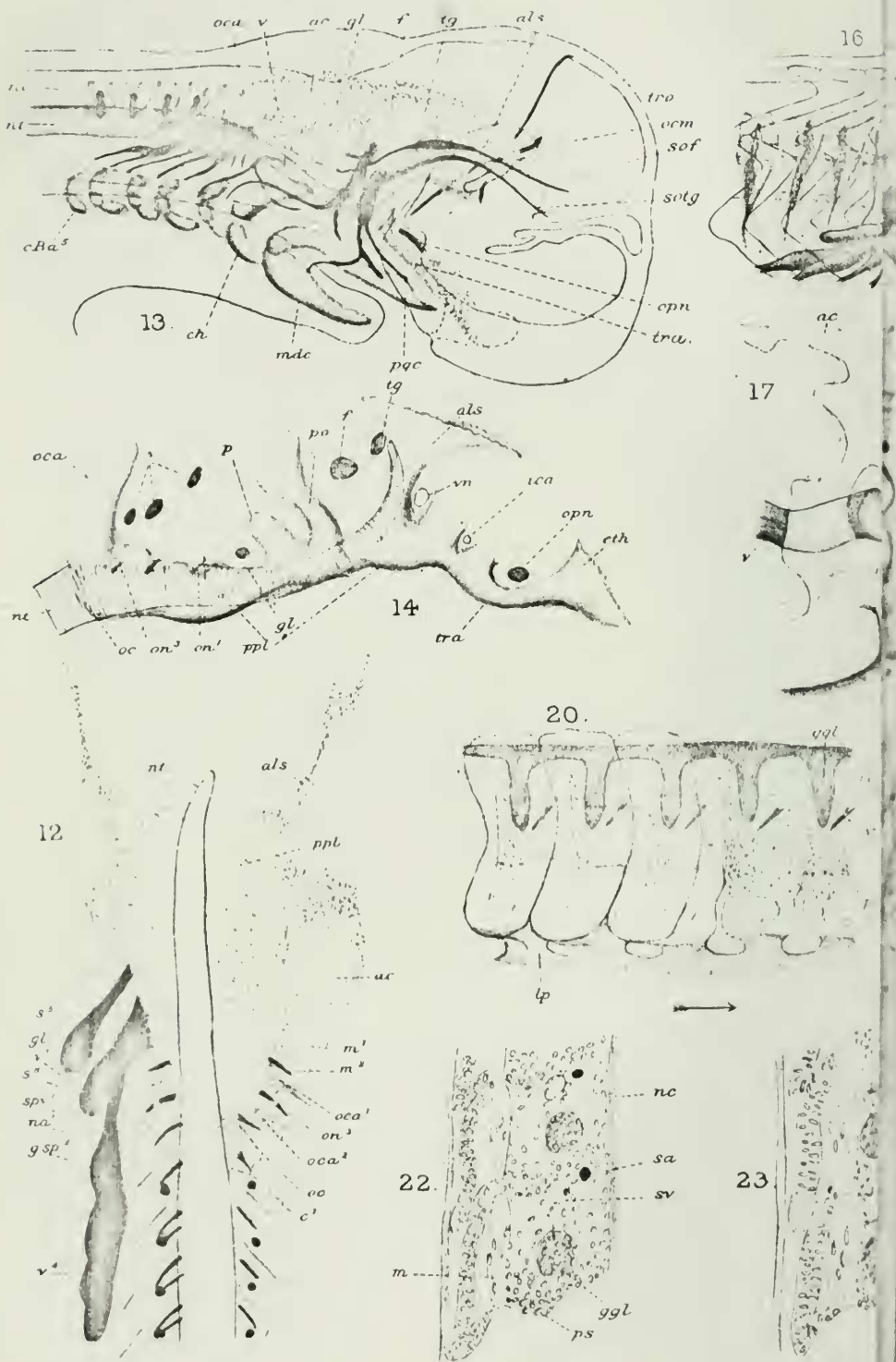
In 1867 Verrill (28) erected the sub-family Phelliinæ of the family Actinidæ, defining it as follows: "Column elongated; covered with a persistent thickened epidermal deposit, except that, near the margin and sometimes close to the base, the

surface is naked and may be retracted within the thickened portion. Acontia very few and seldom emitted—perhaps entirely wanting in some species." In his definition of the genus *Phellia* Verrill says of the acontia that they are "sparingly emitted from the mouth and from pores near the base," and in his description of a large and handsome species, *Phellia panamensis*, he notes among other characters the following: "Column . . . capable of contracting into the form of a tall cone by involving the summit. . . . Tentacles about 96 in number, the 12 inner ones large and stout. . . . In dissecting a large specimen it was found that the 12 septa corresponding to the 12 large inner tentacles, are much larger than the others, with the inner edges strongly thickened and muscular, and bear the large convoluted ovaries throughout nearly their whole length, while the intervening septa are very narrow, not thickened, and bear no sexual organs." This is the first recorded account of the internal anatomy of a member of the genus *Phellia*. It should be observed that Verrill keeps the *Phellinae* distinct from his sub-family *Sagartinae*.

In 1884 Andres (1) makes the *Phellidae* a sub family of the family *Actininae*, keeping them separate from the *Sagartiidae*, and includes in the sub-family the genera *Octophellia*, *Phellia*, *Ilyactis*, *Chitonactis* and *Ammonactis*. Of these *Octophellia* does not appear to have been heard of again, and the three last have been removed from the sub-family on anatomical grounds. Andres' definition of the *Phellinae* is founded on external characters, but in his account of the anatomy of Actinians he takes *Phellia limicola* as an illustration, and figures and describes six pairs of complete and fertile mesenteries with labial and parietal mesenterial stomata; eighteen pairs of infertile incomplete mesenteries. In the light of more recent work the accuracy of some of his anatomical statements is open to suspicion. Thus, he omits to figure or describe the characteristic parietal muscles of the mesenteries; he figures and describes, correctly enough, the muscle banners of the large longitudinal retractors of the twelve primary







mesenteries, but also figures muscle banners on the secondaries, a feature which, if it occurs, is unique among the species anatomically investigated. New species were added to the genus, but no additional anatomical investigations were made on it till, in 1897, Kwietniewsky (22) described and gave a short anatomical account of *Phellia ternatana*, and in the same year Haddon (16) and Maguire (24) did the same for *P. sollasi* from the island of Fumafuti. In the following year Kwietniewsky (23) described the anatomy of *P. ambo-nensis* and Haddon (17) that of *P. vermiformis* and *gansapata*. The result of these several investigations may be summarised by saying that they corrected Gosse's and Verrill's error in attributing cinclides to the genus; they confirmed Verrill's observation that gonads are borne only on the twelve primary and perfect mesenteries; they drew attention to the small size and imperfect development of the remaining mesenteries; showed that they have only parietal and no longitudinal retractor muscles, and that they can be arranged in secondary, tertiary and quaternary orders, but the last order is always incomplete. Kwietniewsky suggested, as an addition to the definition of the family, that the fourth cycle of mesenteries is only represented by half the full number, since the quaternary septa are absent in all the loculi adjacent to the primary septa. The authors, furthermore, agreed in describing a mesogloal sphincter muscle, extending over the upper third of the column, thicker below in the scapus, but thinner above in the capitular region. The outcome of this work was a new definition of the Phelliinæ by both Kwietniewsky and Haddon, both now including the sub-family in the Sagartiidae. I quote Haddon only, as the two authors agree in all but unessential particulars. "Phelliina" (sic, Kwietniewsky gives Phelliinæ, Verrill); "Sagartiida, with usually an elongated column, the capitular part of which is delicate and extensile; body-wall provided with a cuticle, but without any solid or hollow processes, such as tubercles, vesicles or suckers; no cinclides. Tentacles simple, neither very numerous nor very long. Only six pairs of perfect

mesenteries which alone are fertile. The remaining mesenteries are usually freely developed. The retractor muscles are very strongly developed on the primary mesenteries. Acontia usually feebly developed, and emitted only through the mouth. Strong mesogloal sphincter muscle." Similar as their definitions are, the two authorities differed widely in respect of the forms included in the sub-family. Kwietniewsky, and with him Simon and Carlgren, included *Chondractinia*, *Hormathia*, *Chitonactis* and other forms, which Haddon placed apart in another sub-family *Chondractiniinae* on the good ground that, whereas in *Phellia* the primary mesenteries alone are fertile, in the *Chondractiniinae* they are always sterile, and only the well-developed lesser mesenteries are fertile. There can be no doubt that the judgment of the British author is correct.

Recently, in 1911, Wilsmore (31) has given a careful anatomical description of *Phellia brownii* and *capitata* from New South Wales, in which she has confirmed and extended the observations of her predecessors.

As may be inferred from this short historical preface, the genus *Phellia* has received a larger share of attention to its anatomical character than most other genera of Actinians. None the less, I am again dealing with the subject at some length. Among the Actinians collected by Dr. Willey in New Guinea were five species referable to the sub-family, four of which I have placed in the genus *Phellia*, and for the fifth I have erected a new genus. It was not possible to determine the systematic position of the forms except by a study of the anatomy; dissection gave few results, so I had recourse to sections, and in the study of these my attention was directed to a number of details, from which, as I think, inferences as to the systematic position and affinities of the *Phelliinae* may legitimately be drawn. Therefore, although I must necessarily traverse a considerable extent of old ground, I have not scrupled to set out my observations in full, and must ask the reader's pardon if some parts of them are of no great novelty and interest.

Accepting Haddon's exclusion from the Phelliinæ of the forms which he has placed in the Chondractiniinæ, and accepting provisionally his definition of the former group, I will proceed to the discription of the species contained in Dr. Willey's collection, reserving further discussion for the latter part of this paper.

GENUS PHELLIA, Gosse.

PHELLIA CASTANEA, n. sp.

Single, fixed (?). Scapus minutely transversely wrinkled and furrowed; covered by a chestnut-red cuticle in which are imbedded numerous grains of reddish, black, and colourless and transparent quartz sand. The upper sixth of the scapus introverted in contraction. Column cylindrical, tapering slightly towards the base. Capitulum in contracted state very short, longitudinally ridged. Base or physa thin, concave; in the single specimen examined filled with quartz sand impacted with mucus into a solid mass. Tentacles 24, in two cycles of 12 and 12; short, conical, deeply transversely wrinkled in contraction. Peristome deeply concave, very thin. Mouth gaping.

Length of contracted specimen, 9 mm.; greatest diameter, 5 mm.; diameter at base, 3.3 mm.

Locality: Rakaiya, New Britain.

The above description, limited to external characters, requires the following explanation. In many species of Phellia a considerable part of the upper or distal part of the column is introverted in contraction, as in *Edwardsia*, and Wilsmore (31) describes the whole of the involuted portion as the capitulum. This description, I take leave to think, is an error. The terms "capitulum," "scapus," and "physa" were first used by Gosse (14) in his definition of the genus *Edwardsia*: "Column long, slender, cylindrical, divided into three distinct regions, of which the two terminal are retracted within the central one. Anterior region forming a short thick pillar (capitulum) of less diameter than the central, and more delicate. Central region (scapus) covered by a

skin (epidermis) more or less thick and opaque. Posterior region (physa) thin, pellucid, inflatable like a bladder; imperforate (?)."

Haddon (15 and 17) and others have extended the use of these terms, without much discretion, as I think, to the description of Actinians, in which there is no very obvious distinction of the column into three, or even into two regions. Gosse does not use the terms "capitulum" and "scapus" in his definition of the genus *Phellia*, but his figures (loc. cit., Pl. 7, figs 1 and 2; Pl. 12, fig. 8) show as clear a division into an anterior more delicate region and a central region covered by an epidermis as in any of the *Edwardsia* illustrated in the same plates. It seems legitimate, therefore, to apply the terms "capitulum" and "scapus" to the *Phelliidae*, but with their original signification. The term "scapus" should be limited to that part of the column clothed by an epidermis, and the term "capitulum" to the distal part of the column not so clothed and of a more transparent and delicate structure. That Gosse recognised this distinction is shown by his account of the habits of *Edwardsia callimorpha* (*beautempsii*) loc. cit., p. 257: "If rudely touched the disc was suddenly withdrawn; the capitulum, and then the upper two-thirds of the scapus, disappearing in rapid succession by a process of introversion." The capitulum, therefore, is not that part of the column introverted in contraction, but the more delicate distal region of the column, not covered by an epidermis. The two regions are distinct enough in *Phellia castanea*, but the capitulum is very short and so deeply infolded in contraction that its limits are not easy to determine in transverse sections. It is recognised by the thinness of the mesoglaea; the small size of the sphincter muscle, here reduced to a few circular fibres imbedded in the mesoglaea; and the low columnar layer of ectoderm, with a distinct external limiting membrane but no trace of an epidermis. The introverted portion of the scapus is readily distinguished by the abundant epidermis, reddish-brown in stained sections; by the sparse and modified ecto-

derm underlying the epidermis; and by the thickness of the mesoglœa, which, in this region, is specially thickened to form six longitudinal ridges corresponding to the exocœles of the six pairs of primary mesenteries. From these ridges secondary branched projections radiate towards the centre of the cavity of introversion, and each whole ridge with its projections seems to correspond with the "soft nose-like projections of the capitulum," described by Wilsmore (31) in *PHELLIA browni*.

In *P. castanea* the sphincter muscle is mesoglœal; not very strongly developed, thickest at the rim of the introverted region of the scapus and thinnest in the capitulum. It is somewhat thickened at the bases—i. e. the morphological inner sides—of the six mesoglœal ridge-like thickenings described above, but it does not extend deeply into these thickenings nor into the secondary projections from them, as described by Wilsmore for *P. browni*.

MESENTERIES.—These are best described as macromesenteries and micromesenteries.

THE MACROMESENTERIES are twelve in number, forming six pairs, two of which are directives. All the macromesenteries are well developed, attached throughout its length to the actinopharynx; are provided with well-developed parietal muscles; and bear conspicuous longitudinal retractor muscles. The latter are reniform in section; have the usual Actinian arrangement, that is to say, they are *dos à dos* in the directive, *vis à vis* in the remaining mesenterial pairs; and the mesoglœal pleats to which the muscle fibres are attached give a characteristic dendritic figure in transverse section. In the distal three-quarters of the column the mesenterial arrangement does not require any special description, but, in the proximal third the macromesenteries in regular sequence diminish in size and lose first the large reniform muscle banner lower down the plicated free edge with its mesenterial filament, and finally on the inner wall of the column are reduced to relatively low ridges in which only the parietal muscles can be distinguished.

Faurot (13) has remarked that the "Actinies pivotantes," a group in which he includes the genera *Edwardsia*, *Halcampa*, *Peachia*, *Ilyanthus*, and *Eloactis*, are characterised by the gradual diminution in width of the macromesenteries towards the basal end, and by the diminution in size and final disappearance of the longitudinal retractor muscles in the narrow ends of the mesenteries. He has also (loc. cit., p. 91) laid stress on the fact that in *Halcampa* (as was first observed by R. Hertwig (19)), *Peachia* (= *Siphonactis*), *Cereus pedunculatus* (= *Sagartia bellis*), and *Chitonactis coronata*, two couples¹ of mesenteries, namely, those which appear fifth and sixth in order of development, are recognisably narrower and shorter than the other eight protocnemes: "Il en résulte une disposition qui, sur les coupes transversales, permet de reconnaître facilement les huit premières cloisons formées chez l'embryon. Cette disposition existe aussi, quoique moins évidente, sur les Hexactinies adultes."

Similar observations have been made by G. N. and A. F. Dixon (10) on *Bunodes verrucosa*, *Actinia mesembryanthemum*, and *Cereus bellis*.

A similar embryonic condition of the protocnemes is very clearly exhibited in the basal third of *Phellia castanea*, and in other undoubted members of the genus *Phellia* described in this paper. As is shown in Pl. 4, fig. 15, at a distance of about one-third of the length of the contracted specimen from the basal end the ventral members of the dorso-lateral and ventro-lateral macromesenterial pairs diminish in size; the large, reniform muscle banner is reduced and finally disappears; the plicated free edge of the mesentery becomes narrower, loses the filament, and eventually dies out altogether, so that a transverse section taken somewhat below this level shows only eight macromesenteries with the muscle banners oriented as in *Edwardsia*. At a somewhat lower level the two directive pairs of macromesenteries follow

¹ Throughout this paper I use the terms "pair" and "couple" in Faurot's sense.

snit (see Pl. 4, fig. 19, for *P. phassonesiotes*), leaving only four macromesenteries with muscle banners, and these correspond with the two couples of protocnemes formed first in Actinian development. Close to the base all the macromesenteries are reduced, and are recognisable only by the somewhat larger size of their persistent parietal muscles.

This reduction and final disappearance in regular succession of the muscle banners and mesenterial filaments in certain macromesenterial couples is of importance, for it suggests that in *Phellia* and in the other genera enumerated by Faurot and the Dixons the stages with four and eight protocnemes are of some duration in ontogeny, and that the two mesenterial couples which make up the hexamerous arrangement are added comparatively late in life. It also has the practical advantage that it enables one to determine the orientation of the animal, and to define the "dorsal" or sulcular and "ventral" or sulcar aspects with much greater precision than is possible in most hexamerous Actinians.

Previous authors have noted the fact, and it has become part of the definition of the sub-family Phelliinæ (Haddon (17), Kwietniewsky (22)), that gonads are borne only on the twelve macromesenteries. This is true of *Phellia castanea*, with the difference that in the single specimen contained in Dr. Willey's collection there are only ten pairs of fertile mesenteries, the ventral members of the ventrolateral pairs being sterile. The specimen is a male, and in every fertile mesentery some of the sperm-follicles contain spermatozoa, others showing only the earlier phases of spermatogenesis. It is possible that the absence of gonads in a single couple of macromesenteries may be an individual peculiarity, or that in this case the development of the germ-cells in this particular mesenterial couple may have been retarded. But I could find no trace of germ-cells in this sterile couple, and am inclined to the opinion that these, the latest of the macromesenteries to be developed, are definitely and permanently sterile in *P. castanea*, but must admit that the evidence in favour of this opinion is not very definite.

It is noticeable that in *P. castanea* the ventral members of the dorso-lateral and ventro-lateral pairs are the only macromesenteries that give off acontia, therefore the last-named organs are confined to the macromesenteries latest in order of development. In two other species in Dr. Willey's collection undoubtedly belonging to the genus *Phellia* none of the macromesenteries bear acontia, but according to Maguire (24) all the macromesenteries bear acontia in *P. sollasi*. Neither Kwietniewski (22 and 23) nor Wilsmore (31) makes any definite statement on this subject with reference to the species that they have respectively studied. It would seem that the distribution and development of acontia varies within wide limits in the genus.

There are both labial and parietal mesenterial stomata, the former minute, the latter of considerable size. Both lie at about the same level, close below the oral disc. The acontia pass freely through the parietal stomata from one inter-mesenterial space to another.

MICROMESENTERIES.—These are sixteen in number, all of them small, and for the most part consisting of low ridges projecting from the body-wall into the cœlenteron, each ridge consisting of the central mesogloæal lamina with lateral folds, to which the muscle fibres of the parietal muscles are attached, the whole covered by undifferentiated endoderm. The micromesenteries, however, are of different sizes, and some of them are so far advanced beyond the others in development that they bear mesenterial filaments, acontia, and even traces of longitudinal retractor muscles. Their structure and arrangement require detailed consideration.

There are three micromesenteries in each dorso-lateral sextant¹: of these the median, marked *dl. 1* in Pl. 4, figs. 14, 15, 16, is the largest, bears a short mesenterial filament, trefoil-shaped in section, has a trace of a longitudinal

¹ The six pairs of macromesenteries divide the cœlenteron into six equal radial exocœlic chambers, which may be conveniently described as sextants, and I shall use this name for descriptive purposes throughout this paper.

retractor muscle, and gives off an acontium; the most dorsal of the three, marked *dl. 2* in Pl. 4, figs. 14, 15, 16, has a well-developed parietal muscle, but bears neither filament nor acontium; the most ventral of the three, marked *dl. 3* in Pl. 4, figs. 14, 15, 16, is very small, and even the parietal muscle is rudimentary.

There are similarly three micromesenteries in each lateral sextant: of these the median, marked *l. 1* in Pl. 4, figs. 14, 15, 16, is the largest, and bears filament, acontium, and trace of the longitudinal retractor muscle; the most dorsal of the three, marked *l. 2* in Pl. 4, figs. 14, 15, 16, bears an acontium, but a mere trace of the filament and longitudinal retractor muscle; the most ventral, marked *l. 3* in the same figures, is very rudimentary.

There are two micromesenteries in each ventro-lateral sextant: of these the more ventral, marked *vl. 1* in Pl. 4, figs. 14, 15, 16, is the larger, and bears acontium, filament, and trace of longitudinal retractor muscle; the more dorsal, marked *vl. 2* in Pl. 4, figs. 14, 15, 16, has a well-developed parietal muscle but no trace of filament or acontium.

Pl. 3, fig. 12 A, represents a transverse section of the median micromesentery of the right-hand lateral sextant magnified 385 diameters. The section passes some little distance above the level of the enterostome, and shows the mesenterial filament, trefoil-shaped in section, the acontium, and at *l.r.m.* the slightly plicated edge of the mesogloæal lamina, to which longitudinal muscle fibres, appearing as dots in section, are attached. Pl. 3, fig. 12 B, is a similar section of the micromesentery marked *l. 2* in Pl. 4, fig. 15, i. e. the most dorsal of the three micromesenteries in the right lateral sextant. This section is taken at a considerably lower level in the column than that depicted in Pl. 3, fig. 12 A, and is some distance below the enterostome. It shows the rudiment of an obscurely tri-lobed filament, which, three sections lower down, is produced laterally into an acontium and then disappears, and at *l.r.m.* the slightly plicated edge of that part of the mesogloæal lamina lying between the parietal muscle and the

filament, to which longitudinal muscle fibres are attached as in Pl. 3, fig. 12 A.

There can be no doubt that in both sections the muscle fibres *l.r.m.* represent the rudiment of the longitudinal retractor. The two sections, though taken at different levels, are placed in their relative position to one another, and it will be seen that the longitudinal muscles are *vis-à-vis*, so there can be no doubt that these two micromesenteries, though in different stages of development, constitute a "pair," and have the normal arrangement of the longitudinal retractor muscles. Similarly, in the dorso-lateral sextant, the orientation of the rudimentary retractor muscle fibres on *dl. 1*, Pl. 4, fig. 15, show that they are paired with *dl. 2*, and in the ventro-lateral sextants there is similar evidence that *vl. 1* pairs with *vl. 2*.

In making the identification of the rudiment of the longitudinal retractor muscle in certain micromesenteries, I dissent from the view put forward by Kwietniewsky (23) that the musculature on one side of a micromesentery is longitudinal and on the other side parietal. As is shown in all the figures of transverse sections 14-24, musculature of the macromesenteries consists of the large, reniform expansion nearer to the axial than to the peripheral end of the mesentery, and confined to one side of it. This is the longitudinal retractor, and separated from it by a long tract in which the mesentery is very thin and usually without any trace of mesogloal plications or muscle fibres, is a muscle symmetrically disposed on both sides of the peripheral end of the mesentery. In a true transverse section the fibres of these latter muscles are cut through obliquely, and equally so on both sides. In this respect there is no difference between the more peripherally situated muscle on one side or the other. These obliquely disposed fibres, distant and very distinct from the longitudinal retractors, are associated with the body-wall or paries and may properly be called parietal. When comparison is made with a micromesentery it is clear that, with the exceptions above described, the only muscles of the latter are the equivalents of the

parietal muscles of the macromesenteries, and that, as a rule, longitudinal musculature is absent. In many Actinians e. g. conspicuously in *Siphonactis*, the parietal muscle on the side opposite to that which bears the longitudinal muscle is specially well developed and borne on a distinct offshoot of the mesogloea. When thus differentiated it constitutes the parieto-basilar muscle of Hollard.

I should add here that in all the micromesenteries in which they are present the filaments are very short. The filament depicted in Pl. 3, fig. 12 A, extended over twenty-two sections 10μ in thickness and therefore had a length of only $\cdot 22$ mm. The rudimentary filament of Pl. 3, fig. 12 B, was only $\cdot 1$ mm. in length.

I have given a lengthy description of the micromesenteries because the detailed study of them has convinced me that, in the genus *PHELLIA*, they are formed in regular sequence, not in couples of pairs as in most dodecameral Actinians, but in couples of singles; one member of a couple right, the other left, of the median plane passing through the directives. The account given above affords sufficient evidence that the micromesenteries *dl. 1*, *l. 1* and *rl. 1* are the first to be formed in each sextant. The inner end of each of them has grown centripetally and has developed a trilobed filament, an acontium and a rudimentary retractor muscle. The next oldest micromesenteries in developmental sequence are *dl. 2*, *l. 2* and *rl. 2*. Of these the couple *l. 2* is the most advanced in development and has acquired rudimentary filaments, acontia and rudimentary retractor muscles, these structures appearing at a considerably lower level than in the case of *dl. 1*, *l. 1* and *rl. 1*. I have shown that *l. 2*, *l. 2* are on the way to form pairs with *l. 1*, *l. 1*, and there can be little doubt that the couples *dl. 2*, *rl. 2*, though they have not acquired filament, acontia or retractor muscles, stand in a similar relation to the couples *dl. 1*, *rl. 1*. The rudimentary couples *dl. 3*, and *l. 3* are unpaired.

The interest of these observations lies in the fact that, though they eventually become paired, the micromesenteries

of *Phellia* are, at their initiation, formed in couples and thus repeat the developmental rhythm characteristic of the protoconemes of all the Dodecactiniaria. To this extent they resemble the micromesenteries of the Edwardsiæ, which, as I have recently shown (4) are formed in couples of singles, but differ from those of *Phellia* in never forming pairs. In *P. castanea* the mesenterial arrangement is nearly that of *Halocampa*, but differs in that there are two additional micromesenterial couples, one in the dorso-lateral and one in the lateral sextants, and also in the fact that the fertile macromesenteries do not correspond in the two genera. There is another and considerable difference in that the adult *Halocampa* has only twelve tentacles, half as many as the number of mesenteries, whereas in *P. castanea* and in the other species of *Phellia* described anatomically in this paper and by other authors the number of tentacles corresponds closely to the number of mesenteries.

The tentacles in *P. castanea* are short, simply infolded over the oral disc and not invaginated in retraction as are the tentacles of *Edwardsia*. As ascertained by the study of sections of the retracted specimen they are twenty-four in number, arranged in three cycles of $6 + 6 + 12$, those of the two innermost cycles being endocœlic and the twelve tentacles of the outermost cycle exocœlic. There are no tentacles in connection with the rudimentary micromesenteries in the dorso-lateral and lateral macromesenterial exocœles, hence the total number of tentacles falls short by four of the total number of mesenteries. As seen in transverse sections of the retracted specimen, the large endocœlic tentacles communicate with the cœlenteron by wide openings, which, in the case of the primary endocœlic tentacles of the innermost cycle, occupy the whole width of a chamber included in a macromesenterial pair, and, in the case of the secondary endocœlic tentacles occupy nearly the whole space between two adjacent macromesenterial pairs. Consequently, the exocœlic tentacles forming the outermost cycle are squeezed in at the edge of the disc between the bases of the primary and secondary

endocœlic tentacles, and their cavities communicate by narrow openings with the cœlenteron. The capitular extremities of the rudimentary micromesenteries of the dorso-lateral and lateral macromesenterial exocœles extend for a short distance into the basal parts of the cavities of the more ventral exocœlic tentacles in those chambers and come into close relation with the macromesenteries contiguous to them. The significance of these details will be pointed out later on in this paper.

The ectodermal musculature of the tentacles is not specially well developed in *P. castanea*. On the outer faces of the tentacles it is weak, the longitudinally disposed muscle fibres being supported by very short processes of the mesoglœa and extending downwards as far as the upper edge of the capitulum. On the inner or oral aspect of the tentacles the ectodermal musculature is much more highly developed in the endocœlic tentacles; its fibres, supported by conspicuous branched processes of the mesoglœa, diverge outwards at the base of each tentacle and are inserted on the adjacent radial lines marking the attachments of the macromesenteries to the disc. The muscle fibres of the inner faces of the exocœlic tentacles converge to form a distinct bundle inserted close to the attachment of the adjacent macromesentery to the edge of the peristomial disc. The effect of this disposition is that the tentacles are flexed inwards towards the peristomial disc by the contraction of the strong muscle fibres of their adoral surfaces, whereas the weaker muscles of their aboral surfaces come into play during the slower movements of expansion. It is further evident that the insertions of the adoral bands of tentacular muscles on the upper edges of the macromesenteries ensures the co-adaptation of function of the powerful longitudinal retractors of the macromesenteries with the muscles of the tentacles and disc. When the former contract they forcibly pull down the disc and bring about the introversion of the capitulum and upper region of the scapus; the muscles of the inner faces of the tentacles, contracting at the same time, bend the tentacles inwards over the peristomial

disc, and as invagination proceeds cause them to assume the dependent vertical position with tips downwards shown in Pl. 3, fig. 1, *t*.

The ectoderm of the tentacles is abundantly furnished with nematocysts. These are all of the small spiral variety [type I of Matthai (25), spiral cnidæ or cnidæ cochleatæ of Gosse], measuring 39.5μ in length by 5.2μ in diameter (see Pl. 3, figs. 6 and 7). I have found no other kind of nematocyst in the tentacles of any of the *Phelliinæ* that I have examined. Between the nematocyst-laden layer of the ectoderm and the muscular layer is a fibrillar nervous layer, very thin on the external faces of the tentacles where the muscular layer is weakest, but much thicker on the inner faces where the muscular layer is strongest. The nematocysts are also much more abundant and more closely crowded together on the inner surfaces of the tentacles. These relations, taken in conjunction with the fact that one never finds the spiral thread extended, suggest that this type of nematocyst is tactile rather than urticant in function. Concerning this question, and the structure and development of the different types of nematocysts found in Actiniaria, I shall have something to say in another place.

It may be noted here that *P. castanea* has fewer tentacles, and correlated with this fewer mesenteries, than any other known species of the genus. *P. phassonesiotes* and *P. allantoides* described in the sequel, have 36 and 44 tentacles respectively; *P. sollasi*, teste Haddon, has 48-54; *P. browni*, teste Wilsmore, has over 40; *P. capitata* has 39, plus several buds; and *P. ambonensis*, teste Kwietniewsky, has 70 tentacles.

The peristome in *P. castanea*, as may be seen in Pl. 3, fig. 1, is deeply concave and the mouth gapes widely. In this it agrees with Gosse's description of *P. murocincta*, the type species of the genus; "disc a deep cup bounded by the thick feet of the inner tentacles" (14, p. 135). This description is in every respect applicable to *P. castanea*, and I am disposed to consider the concave peristome and

gaping mouth as generic characters. Gosse says of *P. gausapata*, "disc a deep cup or funnel," and I gather from Wilsmore's figures that a similar description would be applicable to *P. browni* and *P. capitata*, though she does not make any mention of this feature in her text. The description is certainly applicable to the other species of *Phellia* described in the continuation of this paper. Gosse, it is true, describes *Phellia picta* as having "disc nearly flat or slightly concave," but in a note on this species in the appendix to the 'Actinologia Britannica' he says, with reference to additional examples sent to him from Banff: "The epidermis is very thin and deciduous and altogether the species seems intermediate between the true *Phellia* and such *Sagartia* as *coccinea*." It is therefore probable that Gosse's *Phellia picta* is not a member of the genus *Phellia*.

The peristomial disc proper, that is to say, the area between the mouth and the bases of the tentacles is very thin in *P. castanea*, and I could find in it no trace of muscle fibres or nervous layer, nor are any nematocysts to be found in this region. Kwietniewsky (22 and 23) and Wilsmore (31) give elaborate descriptions of the musculature of the "disc" which are perfectly consistent with the account given above of the musculature of the bases of the tentacles, but I do not find, either in *P. castanea* or in the other species that I have examined, that the muscles extend over the peristome as defined above. The difference between my account and theirs probably consists in this, that they include the whole area between the mouth and the upper edge of the capitulum under the term "disc," whereas I only include the area between the mouth and the bases of the tentacles in the term "peristome." My use of the term is more consistent with Gosse's description of *P. mureocincta*, quoted above.

The actinopharynx, as may be seen in Pl. 3, fig. 1, is large; its walls transversely wrinkled, probably as the result of contraction. Longitudinal ridges corresponding to the insertions of the macromesenteries are not very prominent.

Dorsally, there is a distinct gonidial groove or sulculus, in which the epithelium is so far differentiated that it contains no nematocysts, very few gland cells, and the ciliated cells are more closely crowded and bear longer cilia than elsewhere. A similar differentiation is found ventrally in the region bounded by the ventral directive macromesenteries, but here the epithelium bulges slightly into the cavity of the actinopharynx; this is probably the result of contraction, and one may say that a ventral groove or sulcus is present, but that the dorsal groove or sulculus is the more clearly differentiated (Pl. 4, fig. 14).

The general features of the mesenterial filaments and gonads are sufficiently well shown in Pls. 3 and 4, figs. 1, 15, and 16, and as far as macroscopical characters go they are normal and require no special description. The acontia are well developed and are loaded with large nematocysts as is shown in Pl. 3, fig. 12. The single specimen of *P. castanea* was very well preserved for microscopical purposes, but I must postpone a description of histological details to another place.

PHELLIA PHASSONESIOTES, n. sp.

Single, elongate; the column divisible into capitulum, scapus and expanded base. Capitulum short; thin-walled. Scapus of leathery consistency; pinkish-brown in colour; thickly encrusted with calcareous sand; its upper sixth introverted in contraction; tapering towards the base. Expanded base firmly adherent below to a piece of dead coral; its free edges folded and puckered. Tentacles 36; the two inner cycles of six and six distinct, the two outer cycles of six and eighteen incomplete and indistinct.

Length of contracted specimen 30 mm.; greatest diameter 6.5 mm.; least diameter near base 3 mm.

A single specimen from Pigeon Island, New Britain. The specific name is derived from the locality; *φάσσα*, a pigeon; *νησιώτης*, an islander.

The expanded base of this species may also be described as a physa, but I have hesitated to apply this name to it because it can hardly be brought under Gosse's original definition as "thin, pellucid, inflatable like a bladder," and it is adherent. As shown in Pl. 3, fig. 2, it is of the same pinkish-brown colour as the scapus, and has a few grains of sand attached to it, so that it can scarcely be distinguished from the scapus on external examination. Histologically, however, it presents very different characters. The mesogloea of the scapus is pitted and furrowed in every direction, and in section appears to be produced into numerous lobed processes covered by a cubical or very low columnar ectoderm, which is everywhere externally covered by the brown friable and apparently structureless layer called the "epidermis." In the region of the expanded base these characters change somewhat abruptly. The mesogloea, though thickened in some places, is generally thin; its surface is smooth, and not produced into lobed processes; the ectoderm is thick and composed of elongated columnar cells, amongst which are claviform granular gland cells; there is a well-marked external limiting membrane, staining blue in picro-indigo-carminé; but the yellowish-brown epidermis is absent. This histological differentiation is apparent both on the face and on the adherent surface of the basal expansion.

MACROMESENERIES.—These, as in *P. castanea*, are twelve in number, with two pairs of directives, and the reduction and disappearance of the muscle banners of couples V and VI just below the level of the enterostome, and further down the reduction and disappearance of the muscle banners of couples III and IV is very well marked, and is clearly shown in Pl. 4, figs. 18 and 19. All the macromesenteries are fertile, the single specimen being a male. I could not find any evidence of acontia being given off from the macromesenteries. The longitudinal retractor muscles are of very large size, and markedly reniform in transverse section, the reniform outline having a deep hilus, within which the mesentery is attached. The dendritic character of the mesogloéal

folds bearing the muscle fibres is pronounced and characteristic, and I have tried to represent it faithfully in Pl. 4, figs. 17, 18, and 19, but the drawings are on too small a scale to bring out all the details.

There are distinct labial and parietal stomata in all the macromesenteries; the former small, the latter of considerable size, and at about the level of the rim of the introverted scapus. The mesoglœa is thickened at the lips of the stomata.

THE MICROMESENTERIES are twenty-eight in number, arranged as follows: (1) A larger pair in each of the sextants; (2) a smaller pair, lying ventrad of the larger pair, in each of the macromesenterial exocoelæ; (3) a minute and rudimentary unpaired micromesentery lying dorsad of the larger pair in each dorso-lateral and lateral sextant. The last-named bear neither filament nor acontium, scarcely rise above the level of the endoderm, and only are discoverable in the middle of the column, where they have a vertical extent of about 3 mm. All the other micromesenteries bear trefoil-shaped filaments and acontia, and, as in *P. castanea*, the filaments are very short, and occur at different levels in the different cycles of micromesenteries. Thus, taking the measurements from the rim of the introverted scapus, the filaments of the ventral members of the larger pairs commence at about 1.2 mm. below this point: those of the dorsal members of the larger pairs at about 1.6 mm. in the dorso-lateral and lateral sextants, but at 3.6 mm. in the ventro-lateral sextants. The dorsal members of the smaller pairs bear filaments at 6 mm. below the measuring point in the dorso-lateral and lateral sextants, but at 8 mm. in the ventro-lateral sextants. The ventral members of the smaller pairs bear filaments at a distance of 7.5 mm. in the dorso-lateral and lateral sextants, but at 9.5 mm. below the measuring point in the ventro-lateral sextants. The micromesenterial filaments are very short in every case, the longest not exceeding 1.5 mm., and some can only be traced in half a dozen sections $10\ \mu$ thick.

Every micromesentery with a filament bears an acontium at the lower end of the filament. In the smaller mesenterial

pairs the acontia are short and some of them rudimentary, but the acontia of the larger micromesenterial pairs are long and hang down in the cœlenteron, some of them extending to the base, where they end in a tangle of convolutions.

Applying the same reasoning as in the case of *P. castanea* for the determination of the order of development of the micromesenteries, the facts enumerated above suggest that the first micromesentery to be formed in each sextant is the ventral member of the larger pair; then follow the dorsal members of the larger pairs in the dorso-lateral and lateral sextants, and somewhat later the corresponding micromesenterial couple in the ventro-lateral sextants. Next in succession are formed the dorsal members of the smaller pairs, those of the ventro-lateral sextants lagging behind those of the dorso-lateral sextants. Then follow the ventral members of the smaller pairs, those of the ventro-lateral sextants still lagging behind the others. Lastly, we get the rudimentary micromesenterial couples on the dorsal sides of the larger micromesenterial pairs in the dorso-lateral and lateral sextants, but in *P. phassonesiotes* these are not yet developed in the ventro-lateral sextants. If I am right in judging the relative ages of the micromesenteries from the heights at which the filaments appear, the order of succession is the same as in *P. castanea*, but carried to a further stage, and the evidence points to the micromesenteries being formed in couples, the members of adjacent couples subsequently becoming paired.

These inferences as to the order of succession of the micromesenteries are borne out by a study of the tentacles. There are 36 tentacles in *P. phassonesiotes*, arranged in cycles of 6 primary entocœlic, 6 secondary entocœlic, an incomplete cycle of 6 tertiary entocœlic, and an outermost cycle of 18 exocœlic. There are no tentacles corresponding to the rudimentary micromesenteries. It is advisable to postpone the discussion of the probable order of formation of the tentacles in this and the other species of *Phellia* to the latter part of this paper.

As in *P. castanea* the ectodermic musculature of the inner or oral faces of the tentacles is better developed than that of the outer or aboral faces. In general, the musculature of the tentacles is much better developed in *P. phassonesiotes* than in *P. castanea*, and the swollen bases of the tentacles of the inner cycles extend further inwards towards the centre of the disc, giving the appearance of a considerable peristomial musculature. But in this, as in the previously described species, the peristomial wall between the bases of the tentacles and the actinostome is very thin, and no trace of muscular or nervous layers can be detected in it.

The surfaces of the contracted tentacles are deeply wrinkled transversely, and the ectoderm is crowded with somewhat elongate fusiform nematocysts.

The histological condition of the single example of this species was not good, and the tentacles, peristomial disc, and lips of the actinostome were so much crumpled and pressed together that I could not make out details as clearly as in the species previously described. It was evident, however, that the peristome is deeply concave, and the actinostome an elongated oval gaping orifice.

The actinopharynx is relatively short, laterally compressed, its walls thrown into sixteen or seventeen moderately deep longitudinal ridges and furrows, which do not bear any definite relation to the insertions of the macromesenteries. As is shown in Pl. 4, fig. 17, there is a well-marked dorsal actinopharyngeal groove or sulculus, and a less pronounced ventral groove or sulcus. The epithelium was not sufficiently well preserved to allow me to say with certainty that these two grooves are histologically differentiated, but there is some evidence that they are.

The remaining features of the internal anatomy do not call for special description. The acontia are rather thick, and crowded with large nematocysts, nearly all of which were everted. A large scale drawing of these nematocysts is given in Pl. 3, fig. 9.

The sphincter muscle of *P. phassonesiotes* is mesogloæal

and very thin. It is traceable in the greater part, and is best developed in the distal part of the introverted portion of the scapus, and is reduced to a single layer of circularly disposed muscle fibres lying in the thin mesogloea of the short capitulum, but thickens again just below the bases of the tentacles. The endodermic circular muscles are well developed throughout the scapus, and in its distal part coexist with the mesogloecal sphincter, but they are so reduced as to be hardly recognisable in the capitulum.

PELLIA ALLANTOIDES, n. sp.

Single, fixed (?); the column divisible into capitulum, scapus, and physa. Capitulum short; thin-walled. Scapus of a dirty brown colour; thinly encrusted with fine sand; its distal portion deeply introverted in contraction; its surface deeply wrinkled: not tapering towards the base. Physa thin-walled; colourless; inflated and deeply pitted laterally and below. Tentacles 44, in four cycles of 6, 6, 10, 22; the two last cycles incomplete.

Length of contracted specimen, 55 mm.; average diameter, 6 mm.

A single specimen from Uvea, Loyalty Islands.

The specific name refers to the sausage-like shape of the contracted animal.

The thin-walled, colourless, inflated basal portion of this species may legitimately be called the physa. Its edges and lower surface are pitted by a number of round or oval depressions, the shape of which clearly indicates that they were occupied by pebbles or shingle. Some small, rounded fragments of shingle were still sticking in the smaller cavities in the basal end of the physa when the specimen came into my hands, but the pebbles occupying the larger depressions at its sides had fallen out. From the nature of the sand encrusting the scapus one may surmise that the animal was embedded in a layer of soft, muddy sand overlying a bed of shingle, and that it obtained a firmer anchorage than the sand

afforded by adhering by means of its physa to the shingly bed.

In all essential respects this species displays the same anatomical features as the two just described, but there are differences in detail.

The surface of the upper or introverted part of the scapus is thickened to form prominent longitudinal ridges, which, as in *P. castanea*, roughly correspond to the macromesenterial exocœles, and the surfaces of these ridges are again furrowed, so that in section one gets the appearance of a number of branched processes projecting into the central cavity and nearly closing the passage to the mouth. The mesoglœa is greatly thickened in these ridges. The sphincter muscle in this species is largely developed and mesoglœal. It forms a thickish band at the level of the rim of the introverted scapus; is fairly thick from this level as far as the capitulum, sending prolongations into the thickened mesoglœa of the ridges described above. It becomes thinner, but is still a relatively stout muscular band, in the capitulum, and thickens again at the bases of the tentacles.

In this species the muscle fibres of the sphincter are broken up into a number of bands, each of which is surrounded by mesoglœa, thus differing from *P. castanea* and *phassonesiotes*, but resembling *browni*, *capitata*, *ternatana*, and *ambonensis*. I am not, however, inclined to attach much importance for classificatory purposes to the sphincter.

The macromesenteries are arranged in the usual six pairs and all of them are fertile, the single specimen in the collection being a female. The lower ends of the macromesenteries are greatly enlarged, distended with nearly ripe ova, and folded in a most complicated manner, filling up the cœlenteron and distending the proximal half of the scapus. The ovaries, however, do not extend into the physa. The muscle banners are very large in the region of the actinopharynx, and their mesoglœal laminae are beautifully and regularly branched, forming characteristic dendritic figures

in transverse section (Pl. 4, figs. 20, 21). As described for *P. castanea* and *phassonesiotes*, the muscle banners of the fifth and sixth couples of macromesenteries thin out and disappear shortly below the level of the enterostome, and at a somewhat lower level the fourth and third couples follow suit, but the order of their disappearance is not quite as regular as in the two species named. In the physa all the muscle banners are lost, but the macromesenteries still predominate in size. There are small labial and large parietal stomata in the macromesenteries.

The micromesenteries are thirty-four in number, there being six in each dorso-lateral, six in each lateral, and five in each ventro-lateral sextant. In the dorsal and dorso-lateral sextants the middle pair of micromesenteries is the largest, the pair on the ventral side of them next in size, and the dorsal pair the smallest. The dorsal member of the dorsal pair is usually minute. The same rule holds good in the ventro-lateral sextants, but in these only one member of the dorsal pair, and that very minute, is present.

As in *D. phassonesiotes*, some of the micromesenteries bear very short filaments; these are found at different levels, and the detail is almost exactly the same in the two species. Thus, if the highest level, i. e. the most distal from the base, is denoted by A, and successively lower levels by B, C, etc., the ventral members of the larger central pair in each exocœle bear filaments at level A; the dorsal members of the same pair at level B; the dorsal members of the smaller pairs lying ventrad of the larger pairs bear filaments at level C; the ventral members of these smaller pairs at level D, except those in the ventro-lateral sextants, which bear no filaments. The smallest micromesenterial pairs lying dorsad of the larger pairs in the dorso-lateral and lateral sextants and the single micromesenteries occupying a similar position in the ventro-lateral sextants have no filaments. None of the filaments are more than .8 mm. in length.

The acontia are very small, and so rudimentary that they are easily overlooked. They are borne on most of the micro-

mesenteries that also bear filaments, but not on all, and their distribution is irregular. The macromesenteries do not bear acontia. Such as they are, the acontia have the usual structure, and are furnished with large nematocysts. Kwietniewsky (22 and 23) has recorded a similar reduction almost to the point of disappearance of the acontia in *P. ternata* and *ambonensis*, but in *sollasi* (Maguire (24)), *browni*, and *capitata* (Wilsmore (31)) the acontia are long and conspicuous. There is evidently a wide range of variation in respect of these organs in the genus *Phellia*.

The tentacles of *P. allantoides* are relatively large, especially those of the two innermost cycles. They are very muscular, deeply transversely wrinkled in contraction, have distinct muscular nervous and epithelial layers, and the last is crowded with rather elongate spiral nematocysts staining green in picro-indigo-carmin. The relation of the several cycles of tentacles to the macromesenterial and micromesenterial pairs is the same as in *P. phassonesiotes*, but, as the micromesenterial pairs are more numerous in *P. allantoides*, the number of tentacles is also greater. There are no tentacles corresponding to the unpaired rudimentary micromesenteries in the ventro-lateral exocœles.

The ectodermic musculature of the tentacles is specially well developed; it is thicker on their adoral than on their aboral faces, but this difference is not as clearly marked as in *P. castanea*. The muscle fibres are supported by long and thin mesoglœal laminae, which are secondarily folded so as to give a branched appearance in section (Pl. 3, fig. 13), but there is no anastomosis among the branches as described by Kwietniewsky for *P. ternata* and *ambonensis*. The two inner cycles of tentacles are inserted well towards the centre of the disc and the peristome is correspondingly reduced in extent, but, as in the two species already described, the latter is thin, has no muscular or nervous layers, and is deeply concave. The endoderm lining the inner sides of the tentacles and running out in radial lines from their bases towards the actinostome is almost wholly composed of elon-

gated vasiform cells of large size, and filled with deep brown granules of various sizes (Pl. 3, fig. 11). The nature and distribution of these cells, the histological features of which are unexpectedly well preserved, indicate that in the living animal the disc is ornamented with radial stripes of colour, continued up the inner face of each tentacle.

The actinopharynx is short, not more than 4 mm. long in the contracted condition, and is longitudinally furrowed. I could not detect any definite sulcus and sulculus, the grooves at the two ends of the actinopharynx having the same histological features as those on the lateral walls, so far as the state of preservation of the epithelium allowed me to determine.

The only other points that I need call attention to are that the endodermic musculature of the body-wall is strongly developed in all parts of the body-wall, and, as has been noted for other Actinians by Haddon and others, it forms a continuous layer intervening between the peripheral ends of both macromesenteries and micromesenteries and the mesogloea of the body-wall. The mesogloecal laminae of the mesenteries, however, are from place to place continued into the mesogloea of the body-wall. The endoderm muscle fibres are transversely disposed in the capitulum and scapus, but take an oblique direction in the physa. They coexist with the mesogloecal sphincter in the capitulum and introversible portion of the scapus, and here the layer is thin; it is thickest in the scapus, and again thinner in the physa.

The ectoderm of the physa is modified, and consists of tall columnar epithelial cells, among which are numerous club-shaped gland cells with broad external ends, and tapering into fine fibrils internally.

PHELLIA CYLICOIDES, n. sp.

Single, fixed, wine-glass shaped, tapering from the disc downwards to the physa, which is flattened and expanded. Column divisible into capitulum, scapus, and physa. Capi-

tulum half the length of the entire animal; very thin-walled; transparent. Scapes not encrusted with sand; tapering below; transversely corrugated; with firm but not thick walls. Physa expanded; thin-walled; pitted below where attached to shingle. Colour in spirit, white.

Length, 17 mm.; greatest diameter, 8.5 mm.

A single specimen from Uvea, Loyalty Islands. ♂.

Specific name from *κυλικώδης*; wine-cup shaped.

The specimen was not well preserved, the tentacles, disc, and capitulum being damaged and in part so macerated that I could not count the tentacles or make anything of the details in the oral region.

Apparently the capitular wall is very thin and devoid of mesoglœal circular muscle fibres. It was for the most part torn away, but the fragments remaining showed only a very thin lamina of mesoglœa, with very low cubical ectoderm and endoderm cells on its outer and inner surfaces. There is a very thin layer of endodermic transverse muscle fibres. The mesoglœa is striated along its inner border, but I could not detect muscle fibres between the striations. I could not find any trace of a mesoglœal sphincter muscle, even at the bases of the tentacles where the mesoglœa is somewhat thickened.

THE MACROMESENERIES are all fertile and furnished with large longitudinal retractor muscles, reniform in section, and exhibiting the usual dendritic pattern of the mesoglœal processes for the attachment of the muscle fibres. Owing to the damaged state of the oral end I could not determine whether macromesenterial stomata are present. The dorsal directives and the ventral members of the dorso-lateral and ventro-lateral pairs of macromesenteries do not extend nearly so far down as the remainder, and lose their muscle banners at about the level of the middle of the scapulae, leaving only six mesenteries with muscle banners in this region. Still lower down the ventral directives lose their muscle banners, leaving only the macromesenterial complex I and II. Thus, owing to the early reduction of the dorsal directives there is no region

in which the eight "Edwardsian" mesenteries are prominent as in the three species described above. Short but rather thick acontia, furnished with the large nematocysts characteristic of these organs, are given off from the ventral members of the dorso-lateral and ventro-lateral pairs of macromesenteries just below the point where the large reniform muscle banner ends. I could not find acontia in any other macromesenteries nor on any of the micromesenteries.

THE MICROMESENTERIES are twenty-eight in number, and in respect of their arrangement and relative sizes are exactly the same as in *P. phassonesiotes*. But I could only find filaments on the pairs adjacent to the ventral directives and on the micromesentery nearest the ventro-lateral macromesenterial pair on the right side. These filaments are low down, in the region of the enterostome. It is probable enough that other micromesenteries bear filaments at a higher level in the capitular region, but, as the walls of the capitulum were largely destroyed, I was unable to find them. There were no acontia in connection with the three micromesenteries on which I found filaments, and from the absence of portions or convolutions of acontia in the intermesenterial chambers, I judge that none of the micromesenteries bear acontia, or if they do, they are rudimentary.

Owing to their damaged condition I was unable to count the tentacles. So far as their condition permitted of observation they have the same characters as regards musculature, nematocysts, etc., as in the other *Phellia* I have described.

The actinopharynx is long and longitudinally plicated, but I could not distinguish a differentiated sulcus or sulculus. The epithelium is everywhere crowded with long claviform gland cells filled with granules stained green in picro-indigo carmine, their narrower ends external and opening to the surface between the supporting cells.

This species differs from other *Phellia* in the relatively large size of the thin-walled capitulum, in the early reduction of the dorsal directive mesenteries, and, as far as could be

ascertained, in the absence of a mesogloéal sphincter muscle. In all other characters it is a Phellia, and I have not created a new genus for its reception on account of the absence of a mesogloéal sphincter because, owing to its damaged condition, I cannot say anything positive on this point.

DECAPHELLIA, n. gen.

With the characters of Phellia, but the capitulum has no musculature except for a mesogloéal sphincter at its distal extremity, and there are only ten complete macromesenteries bearing longitudinal retractor muscles.

DECAPHELLIA PSAMMOMITRA, n. sp.

Single, fixed (?); the column divided into capitulum and scapus; the base invaginated to form a cup. Capitulum nearly half the length of the entire animal; very thin-walled; inflated; transparent; colourless in spirit; its surface showing ten longitudinal ribs corresponding to the insertions of the macromesenteries. Scapus divided into two regions; the upper region thinner-walled and thickly encrusted with calcareous sand; the inferior region thicker-walled, deeply and completely corrugated, covered by an epidermis but without encrustation. Base deeply concave; covered with a high columnar epithelium. Tentacles 24, in three cycles of 6, 6, 12.

Length, 7.5 mm.; greatest diameter, 2.75 mm.

Two specimens from Lifu, Loyalty Islands.

The specific name refers to the prominent girdle of sand encircling the upper part of the scapus; *ψάμμος*, sand; *μίτρα*, a girdle.

The absence of muscles of any kind on the wall of the greater part of the capitulum and the reduction of the ventral members of the ventro-lateral pairs of macromesenteries are characters of sufficient importance to justify the creation of a new genus for the reception of this species.

Pl. 5, fig. 24, is a drawing of a transverse section passing through the concave peristome and including the bases of some of the tentacles; as the section falls obliquely the thickened lip of the actinostome is included on the right of the section. The figure shows ten complete macromesenteries, having small but well-defined and prominent muscle banners closely attached to the wall of the disc. Dorsal and ventral directives are present with the muscle banners *dos à dos*, and the dorso-lateral pairs are complete. The ventro-lateral pairs are incomplete, as their ventral members, though recognisably longer than the very minute micro-mesenteries, do not reach the disc, and have no trace of longitudinal retractor muscles. Pl. 5, fig. 23, is a transverse section taken through the scapus, a short distance below the enterostome. As the specimen was laterally curved, the section is not truly transverse to the axis of the animal and appears elongated laterally. Nine mesenteries bearing longitudinal retractors are seen, the ventral member of the dorso-lateral pair being reduced on the right side, but not on the left. There is no further reduction, the nine mesenteries in question being continued down to the base without much further alteration except that their mesogloæal laminae are greatly thickened in the lower region of the scapus and the retractor muscle gradually shifts from a more central to a more peripheral position. Thinking that this unusual asymmetry of the macromesenteries must be an individual peculiarity, I made sections of the second example at my disposal and found exactly the same arrangement, and must therefore conclude that the presence of ten macromesenteries bearing retractors in the upper part of the column and the reduction of the number to nine in the lower part is a characteristic of the species. The macromesenteries are perforated by relatively very large parietal stomata at the level of the upper edge of the scapus, but there are no labial stomata, and in this respect also *Decapheilia* differs from *Phellia*, for these perforations are always present in the latter genus.

Neither of the two examples in the collection showed any trace of gonads, and until sexually mature specimens are found there must be some doubt as to the inclusion of Decapheilia in the Phelliinæ, for it is a characteristic of the subfamily that only the macromesenteries are fertile. But from the very small size of the micromesenteries it seems improbable that they should bear gonads in Decapheilia.

Pl. 5, fig. 24, shows the extreme tenuity of the capitular wall. It is composed of a very thin lamina of mesoglœa covered externally and internally by a layer of very flat ectoderm and endoderm cells. There is no trace of transverse endodermic muscular fibres in the greater part of the capitular wall, nor is there the slightest trace of mesoglœal muscle. It is also noteworthy that neither macromesenteries nor micromesenteries exhibit any trace of parietal muscles in any part of the capitulum, but, as Pl. 5, fig. 23, shows, the parietal muscles of all the mesenteries, though not large, are perfectly distinct in the region of the scapus, and correlated with their appearance is the presence of transverse endodermic musculature in this region.

At its extreme distal end, just below the outer cycle of tentacles, the capitular walls thicken, ectoderm, mesoglœa, and endoderm, but especially the mesoglœa, taking their share in the thickening. In this region the endodermic transverse musculature reappears, and there is a distinct mesoglœal sphincter muscle, about .25 mm. in vertical extent. The muscle fibres of the sphincter are few, relatively coarse, and form a single strand.

The micromesenteries are twelve in number; one pair in each sextant. They are tiny and scarcely recognisable projections from the very thin body-wall in the capitulum; in the scapus they acquire the usual feather-shaped parietal muscles, but never attain to any size, and in most places are mere ridges projecting but little beyond the general level of the endoderm. Their free edges are covered throughout the region of the scapus, but never in the capitulum, by a band of modified endodermic epithelium, in which the cells are

more distinctly columnar, and have more deeply-staining nuclei than the adjacent irregularly shaped vacuolated endoderm cells. At about the level of or slightly below the enterostome the micromesenteries are enlarged in depth, the modified epithelial cells invest their sides and tips and become thinner and columnar, their deeply-stained and closely crowded nuclei forming conspicuous objects in section. At a slightly lower level the modified epithelium covering the now swollen end of the mesentery is deeply puckered and thrown into a series of ridges and furrows constituting a "frill" (Pl. 3, fig. 10), which may be traced for a distance of about $\cdot 1$ or $\cdot 2$ mm. and then disappears, the mesentery again becoming a low and inconspicuous ridge. In the region of the frill the swollen extremity of the mesentery gives off a lateral process which is at first slender and somewhat trilobed in section, but after a shorter or longer course is somewhat enlarged in diameter, and displays the histological characters of an acontium, with the usual large nematocysts and gland cells always found in these organs. An acontium of greater or less length is given off from every micromesentery, but none from the macromesenteries.

There can be no doubt that all the elements of the "frill" and the acontium are derived from the endoderm. The acontia are of considerable length relatively to the size of the animal, and pass through the macromesenterial stomata from one intermesenterial space into another, so that their course and origin is difficult to trace in sections: they usually end in a tangled convolution. They can readily be distinguished from the median lobes of the mesenterial filaments by their shape and by the fact that they contain a number of large nematocysts of the type depicted in Pl. 3, fig. 8. These are not present in the mesenterial filaments, but occur in the actino-pharyngeal epithelium.

The tentacles are muscular, the arrangement of the muscle fibres being the same as in the *PHELLINÆ* previously described. The muscle-fibres are relatively large, and the mesogloæal laminae supporting them are unbranched and not very long.

In both specimens at my disposal the tentacles were contracted to mere papillæ and their surfaces deeply transversely wrinkled. The ectoderm is crowded with spiral nematocysts (Pl. 3, fig. 6) so closely packed together as the result of contraction that the other elements of the ectoderm are hardly distinguishable.

By simple inspection one can count twenty-four tentacles arranged in an inner circle of twelve larger alternating with an outer circle of twelve smaller. Sections show that there are three cycles; a macromesenterial endocœlic cycle of six; a micromesenterial endocœlic cycle of six and an outer exocœlic cycle of twelve. The relation of the tentacles to the mesenteries may, therefore, be described as typical. It should be noted that, although the ventral members of the ventrolateral pairs of macromesenteries are incompletely developed, the tentacles corresponding to these pairs are fully developed. In all these characters *Decaphellia* resembles *Phellia*, as also in the distinct deeply concave and thin-walled peristome, in which neither muscular nor nervous layers can be distinguished, and in the widely gaping actinostome.

The actinopharynx is long, extending through the capitulum and well into the upper region of the scapus. Both sulcus and sulculus are well developed, and are lined by an epithelium consisting wholly of attenuated flagellate cells, whose flagella, though not very long, are conspicuously longer than the cilia borne by the rest of the actinopharyngeal epithelium. The mesoglœa of the actinopharyngeal wall is thickened at the insertion of each of the macromesenteries, and the epithelium covering these ridges is also thicker than elsewhere, forming ten longitudinal ridges in the upper moiety, but only nine in the lower moiety of the actinopharynx, for the ventral member of the dorso-lateral pair of the right side is already reduced in the latter region. At the enterostome these nine ridges, covered by a highly glandular epithelium in which there are numerous large nematocysts, are continued into the median euidoglandular lobes of the trefoil-shaped mesenterial filaments.

The base is deeply invaginated and its cupped surface corrugated with irregular ridges and furrows. The ridges are covered with a high columnar epithelium, the cells of which radiate fan-wise from the summit of each ridge and their swollen external extremities are either filled with minute granules staining greyish-blue in picro-indigo carmine or are empty, with more or less collapsed walls. Internally, these cells are prolonged into fine fibres terminating in definite enlargements which I cannot interpret otherwise than as muscles-fibres. The presence of ectodermic muscle-fibres elsewhere than on the tentacles and oral disc is a primitive feature, but in this case there is no ectodermal musculature on the wall of the column as in the Cerianthidæ and in Carlgren's group Protantheæ. The endodermic musculature of the base is highly developed and apparently forms an ill-defined sphincter, some of the fibres of which are here, as elsewhere in the column wall, caught up in and surrounded by irregular processes of the mesoglœa; but one can hardly speak of a mesoglœal sphincter in the base. The ectodermal and endodermal muscle-fibres are connected by very fine but distinct branching fibrillæ, apparently of a nervous nature, which traverse the mesoglœa and some enter into connection with stellate cells imbedded in the mesoglœa.

As is shown in Pl. 3, fig. 5, a tuft of short root-like processes projects from the cavity of the invaginated base. In sections these appear as a tangle of thread-like structures continuous with the cuticular secretion which is everywhere adherent to the surface of the glandular basal ectoderm, but no definite structure could be detected in them. They are doubtless used for attachment. The invagination of the base, a feature common in *Actinange richardi* and other Chondractinidæ, is undoubtedly effected by the powerful longitudinal retractor muscles of the macromesenteries which run right down to and are inserted upon the thick mesoglœal swellings of the lower ends of the macromesenteries just above the spot where the latter are attached to the base. Similar conditions exist certainly in *PHELLIA castanea* and probably

in the other *Phellia* which I have described, but the state of preservation of the latter did not admit of so careful a study of detail as in *Decaphellia psammomitra*. In his definition of the genus *Actinange* Verrill said of the basal disc that it "may be broad and flat, adherent, or it may be bulbous, clasping mud, or it may ensheath the branches of *Gorgonia*, etc." From what precedes it is evident that there is a similar capacity for change of form and adaptability to varying conditions in the *Phelliinae*. When the longitudinal retractor muscles are relaxed the base may assume a bulbous condition as in *Phellia allantoides*, and it is then intermediate between the vesicular physa of the *Ilyanthidæ* and *Edwardsidæ*, and the more or less flat adherent base of the more common *Actinians*.

A transverse section through the scapus of *Decaphellia* is singularly like Faurot's figures of sections of *Halcompa chrysanthellum* (*loc. cit.*, Pl. 8, figs. 2, 3, and 4) the shape and size of the muscle banners of the macromesenteries, the arrangement and convolutions of the mesenterial filaments, and the number and characters of the micromesenteries being strikingly similar. The main differences in addition to the peculiar reduction in number of the macromesenteries in *Decaphellia* are the corrugated external surface and the presence of acontia in the latter genus. The acontia are the dividing factor; were it not for their presence one could scarcely hesitate to include *Decaphellia* among the *Halcompinæ*, and the conclusion that these forms are closely related is irresistible.

This conclusion is strengthened by a consideration of the external and anatomical features of *Halcompactis* (Farquhar, 12). This extremely interesting little New Zealand Actinian has a distinct capitulum; a scapus covered in life by a thin, rough, greyish cuticle; a rounded aboral extremity, not clearly marked off from the scapus, but which one must agree with Farquhar in calling a physa. I gather from Farquhar's account that the tip of the physa is invaginated in certain conditions of retraction. The capitulum is capable of intro-

version. There are six pairs of macromesenteries bearing strongly developed circumscribed retractor muscles resembling those of *Halcampa* and six pairs of micromesenteries alternating with them. Though Farquhar does not say anything on the subject, I gather that the macromesenteries alone are fertile. The tentacles are twenty-four in number; six primary endocœlic, six secondary endocœlic, and twenty-four exocœlic. Acontia are present and are emitted through the mouth only; there are no cinclides. I was in some doubt as to whether I should not place *DecapHELLIA psammomitra* in the genus *Halcampactis*, but *H. mirabilis* has minute suckers on the body-wall, and, according to Farquhar, no sharply-defined circular muscle. These two characters exclude it from the Phelliinæ as defined by Haddon, but, as it has well-developed acontia, it cannot be placed among the *Halcampinæ*. If, as I venture to suggest will be found to be the case, a study of sections should show that there is a distinct though not necessarily "well-defined" circular muscle, *Halcampactis* would certainly find a place among the Phelliinæ, always supposing that its macromesenteries alone are fertile. Should the opposite be the case, and its micromesenteries alone be fertile, it would find its place among the *Chondractiniinæ*, and would connect this sub-family with the *Halcampinæ*. Further details of its anatomy are greatly wanted.

On the Probable Order of Appearance of the Tentacles in the Phelliinæ.

Faurot (13), in his admirable "Études sur les Actinies," gives a detailed account of the order of appearance of the tentacles in *Ilyanthus parthenopæus* and *Tealia (Urticina) felina*. Although the final results are different, owing to the assumption of a secondary decamerall symmetry by *Tealia*, the developmental sequence is fundamentally similar in these two forms, and the rule probably holds good for all the Actiniinæ. In the earliest stage of *Ilyanthus parthenopæus* there are six pairs of mesenteries and

twelve tentacles; six endocœlic and six exocœlic. On the formation of the six pairs of secondary mesenteries a new cycle of six tentacles is formed, prolonging the endocœles of the newly-formed mesenteries. The original exocœlic tentacles are therefore pushed to one side, namely, to the dorsal side, in the dorso-lateral sextants, and to the ventral side in the lateral and ventro-lateral sextants. No new exocœlic tentacles are formed at this developmental phase, but on the formation of the next cycle of twelve tertiary pairs of mesenteries as many new tentacles are formed, prolonging their endocœles. Thus a stage is established in which there are twenty-four pairs of mesenteries and twenty-four endocœlic tentacles corresponding to them, but only six exocœlic tentacles. During this stage, which is of considerable duration, the secondary and tertiary endocœlic tentacles grow more rapidly than the six exocœlic and soon overpass the latter in size. The full number of forty-eight tentacles characteristic of the adult *Ilyanthus parthenopæus* is attained by the formation of eighteen exocœlic tentacles, one for each exocœle hitherto unprovided with these appendages, and the end result is a regular alternation of endocœlic and exocœlic tentacles. This somewhat devious method of arriving at the simple tentacular symmetry of the adult is explained by Faurot on mechanical principles, but these do not suffice, for, if it were simply a question of growth where there is most room for expansion, one would expect each member of a new pair of secondary mesenteries to be formed, one on the one side, the other on the other side of the base of the primary exocœlic tentacle in each sextant of the first developmental phase. If this were so, the primary exocœlic tentacle would become secondarily endocœlic, and a comparable mode of growth actually does occur in the formation of the calcareous septa in Eupsamnid corals (see Pourtalès, 26; Duerden, 11; Bourne, 3). But in the growth of the tentacles in Actiniæ the primary exocœlic tentacles never are included between the members of a pair of mesenteries and therefore never become endocœlic. So far from the line of least resistance

being followed there is, as Faurot clearly shows, a good deal of crowding in some radii, but room for free expansion in others. The peculiar course of development, therefore, must receive an explanation on historical and phylogenetic rather than on mechanistic principles, and some clue is afforded by the study of the relations of the tentacles to the several orders of mesenteries in the Phelliinæ.

The reader will have observed that, in respect of the number and arrangement of the micromesenteries, *Phellia castanea*, *phassonesiotes*, and *allantoides* form a regular series. In the first-named there are sixteen, in the second twenty-eight, in the third thirty-four micromesenteries. In *cylicodes* the number and arrangement is the same as in *phassonesiotes*, and in *Decaphellia psammomitra*, the examples of which were probably adolescent, as they did not contain gonads, there are twelve micromesenteries. In *P. sollasi* Maguire describes fifty-five micromesenteries, and the number is apparently greater in *P. panamensis* Verrill. In all these species there is a distinct dorsi-ventrality in the distribution of the micromesenteries: they are more numerous in the dorso-lateral and lateral than in the ventro-lateral macromesenterial exocœles, and in each sextant the smaller and presumably more recently formed mesenteries appear first on the ventral and later on the dorsal side of pre-existing micromesenterial pairs—a fact which arrested the attention of Kwietniewsky, but he did not attempt to explain its significance.

In the following argument objection may be taken to the fact that I am drawing inferences as to developmental sequences from the comparison of stages observed in different species, and not from stages observed in the development of a single species. I must admit the validity of the objection, but may be allowed to reply that, though it has been desirable, in accordance with the rules of nomenclature, to describe the forms here dealt with as separate species, the possibility of several of them being growth stages of one and the same species is by no means excluded. And even if this

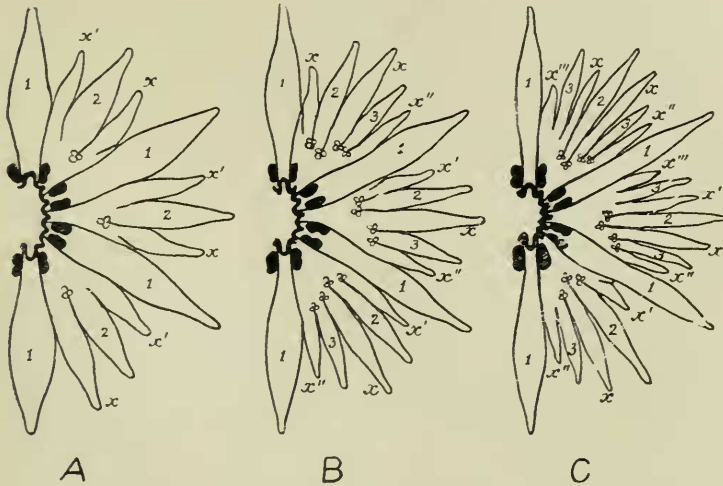
cannot be admitted—I am not inclined to press it—there is much evidence that the *Phellia*, like many other Actinians, are so far pædogenetic that they increase in size and add to the number of their mesenteries and tentacles long after the attainment of sexual maturity. The differences in the number of micromesenteries, therefore, may fairly be taken, not as specific characters, but as indications of earlier or later growth stages in the individuals examined. To this extent, then, they may be dealt with as if they were a developmental series.

The accompanying text-figures are diagrammatic representations of the relations of the tentacles to the mesenteries in (A) *Phellia castanea*, (B) *phassonesiotes*, (C) *allantoides*. In all the diagrams the primary endocœlic tentacles are marked 1, the secondary endocœlic tentacles 2, the tertiaries 3, and the exocœlic tentacles, in the order of their succession, x , x' , x'' , and x''' .

Let us first consider the ventro-lateral sextant in A. There are two mesenteries, of which the larger bears a filament and was the first to be formed. Its fellow is shorter, bears no filament, was formed in close association with the primary macromesentery on the dorsal side of it, and is still closely approximated to it. There are three tentacles, of which the central prolongs the endocœle formed by the two micromesenteries and is the secondary endocœlic tentacle, 2. The most ventral, x , is the original exocœlic tentacle, now displaced ventrally by the formation of the new tentacles on its dorsal side. The most dorsal is the secondary exocœlic tentacle growing out in the space between the smaller micromesentery and the adjacent macromesentery. The lateral and dorso-lateral sextants exhibit the same features, but in both there is a very small micromesentery, which, at the edge of the disc, seems to grow out of the angle between x , the original exocœlic tentacle, and 1, the primary endocœlic tentacle ventrad of it. This single mesentery does not form a boundary to any definite intermesenterial chamber, whether an endocœle or an exocœle, and no tentacle has been formed

in connection with it, for there is no intermesenterial chamber to prolong. The next stage in advance is to be found in the ventro-lateral sextant of B. Here the smaller or tertiary pair of mesenteries has been completed by the formation of a second micromesentery on the ventral side, and the new endocœle is prolonged into the tertiary tentacle, 3, to the ventral side of which appears the tertiary exocœlic tentacle,

TEXT-FIG. 1.



Diagrams showing the relations of the tentacles to the mesenteries in A. *Phellia castanea*; B. *Phellia phassonesiotes*; C. *Phellia allantoides*. 1, 2, 3. Endocœlic tentacles in the order of their development. x , x' , x'' . Exocœlic tentacles in the order of their development. For further description see text.

x'' . In the lateral and dorso-lateral sextants the arrangement is similar, but here a very small, single micromesentery appears at the edge of the disc in the angle between x' and the adjacent primary tentacle dorsad of it. As before, no tentacle has grown out in connection with the unpaired micromesentery. This condition reappears in the ventro-lateral sextant of C, but in the lateral and dorso-lateral sextants the dorsal pair of tertiary mesenteries is completed

by the growth of another micromesentery on the dorsal side of that already existing in the ventro-lateral sextant. Thus there is a new endocœle prolonged into its appropriate tentacle, and a quaternary exocœlic tentacle is growing out between it and the adjacent primary tentacle.

It is sufficiently evident from Magnire's figures that when the number of micromesenterial pairs is increased their development follows the same rhythm.

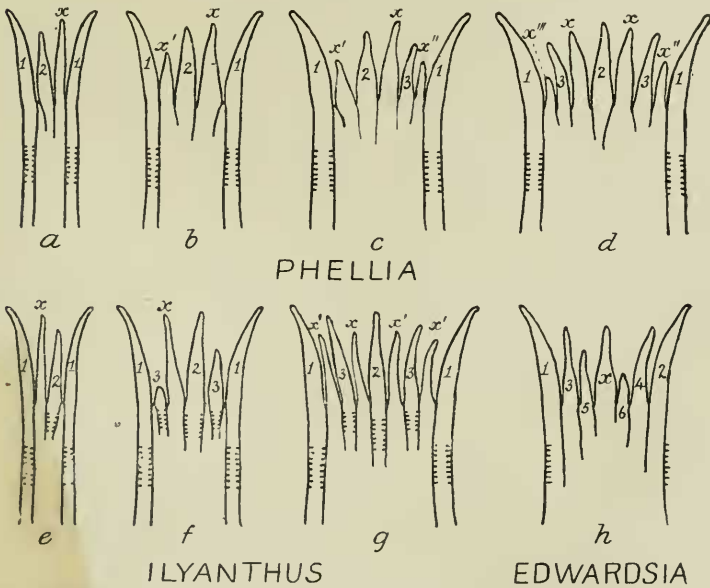
The facts to which I especially wish to draw attention are that the micromesenteries make their appearance in couples and not as complete pairs; that a pair is always established by the growth of an additional micromesentery between the one first formed and the adjacent macromesentery; and that a new endocœlic tentacle does not grow out until the micromesenterial pair of its appropriate endocœle is completed. As a consequence of this successive formation of the parts peripheral growth is gradual, and there is no crowding of the elements in course of formation.

The accompanying series of diagrams, Text-fig. 2, *a-h*, will enable the reader to institute a comparison between the growth processes and succession of the mesenterial pairs and tentacles in *Phellia* and *Ilyanthus*. A tangential section through a single sextant is represented conventionally in each figure; the primary, secondary, and tertiary endocœlic tentacles are lettered 1, 2, and 3; *x* is the primary exocœlic tentacle, and the remaining exocœlic tentacles are lettered *x'*, *x''*, etc., according to the order of their appearance. The different lengths of the mesenteries indicate their respective ages, the longest being the earliest formed.

In *a* is depicted a sextant bounded by two primary macromesenterial pairs in *Phellia*. In the preceding stage (not figured) there was a single endocœlic tentacle. In the stage figured a micromesenterial pair has been formed by the development, first of the longer, then of the shorter of the two micromesenteries shown in the diagram. The secondary tentacle, 2, has grown out from the newly formed micromesenterial endocœle, and has displaced the primary endo-

coelic tentacle, x , towards the right, which is conventionally taken to be the ventral side. In b a secondary exocoelic tentacle, x' , has sprouted between the secondary tentacle, 2, and the adjacent primary endocœle, and at the same time a new micromesentery has been formed to the right of x , apparently from the angle between it and the adjacent

TEXT-FIG. 2.



Diagrams of tangential sections showing the succession of the mesenteries and tentacles in *Phellia*, *Ilyanthus parthenopus* and *Edwardsia cornea*. 1, 2, 3. Primary, secondary, and tertiary endocoelic tentacles. x . The primary exocoelic tentacle. x' - x'' . The remaining exocoelic tentacles according to the order of their appearance. For further description see text.

primary endocoelic tentacle. In c a fellow has been added to the new micromesentery on the right or ventral side, and the two constitute a mesenterial pair of the third order, of which the endocœle is prolonged into the tentacle 3, and an exocoelic tentacle, x'' , has sprouted from the interval between it and the adjacent primary endocœle. At the same time a single tertiary micromesentery has been formed in the angle between

x' and the left or dorsal primary endocœlic tentacle. This is the condition found in the lateral and dorso-lateral sextants of *Phellia phassonesiotes*. In *d* a fellow has been added to the tertiary micromesentery of the left side; the exocœle of the pair so formed has been prolonged into the tentacle, 3, and a new endocœlic tentacle, x'' , is sprouting from the interval between it and the adjacent dorsal primary endocœle. This condition is found in the dorso-lateral and lateral sextants of *Phellia allantoides*. It should be noted that new elements are added alternately on the left (dorsal) and right (ventral) side of the primary endocœlic tentacle, x , which eventually becomes submedian in position, though the actual median tentacle in the sextant is 2, which was formed after x . It should further be borne in mind that, for the sake of economising space, more than one growth stage is included in each diagram: it would take double the number to represent each successive addition of micromesenteries and tentacles.

Diagrams, *e-g*, copied from Faurot (13), illustrate parallel stages in the development of *Ilyanthus parthenopus*. In *e* the two members of a pair of secondary mesenteries with their corresponding tentacle have appeared simultaneously on the ventral side of the primary endocœlic tentacle x . In *f* two pairs of tertiary mesenteries have appeared; one pair, either the larger and earlier in order of appearance, on the ventral side between the secondary tentacle and the ventral primary tentacle; the corresponding rather smaller and later mesenterial pair between the primary endocœlic tentacle x , and the dorsal primary endocœle. Both tertiary endocœles are prolonged into tentacles, but with the exception of the primary exocœlic tentacle x , there are no exocœlic tentacles. There has been no room for these owing to the comparatively rapid formation of the secondary and tertiary mesenteries in pairs, and their development is postponed till the stage represented in *g*, when the three exocœlic tentacles lettered x^1 are formed simultaneously, and make up the full complement of tentacles for the sextant. In this case

the primary exocœlic tentacle x is again submedian in position (but on the dorsal instead of, as in *Phellia*, on the ventral side of the secondary endocœlic tentacle), and the new elements are added alternately on the ventral and dorsal side of it, though not so obviously so as in *Phellia*. But I think it must be conceded that the growth process in the latter genus has every appearance of being the more primitive, and that the peculiar features of the sequence of tentacular growth in *Ilyanthus* receive an intelligible explanation if we regard the second method as derived from the first.

Now *Phellia* has this much in common with *Edwardsia* that in both the micromesenteries are formed in couples of singles. There is no pairing of the micromesenteries in *Edwardsia*, but in *Phellia* the members of adjacent couples combine to form pairs, and it is difficult, though, as I will show, not impossible, to suggest a scheme by which this fundamental difference between the two genera can be bridged over. To make use of Mendelian terminology, it would appear that in Actinian phylogeny a factor for "pairing" was introduced at a certain stage in ontogenetic development. This factor primarily affected the metacnemes; that is to say, all mesenteries formed subsequent to the eight protocnemes, but it carried with it secondary consequences in the relations and mode of succession of the tentacles. For—leaving for the moment out of account the dorsal and ventral directives—as there are no mesenterial pairs in *Edwardsia* there is no division into endocœlic radii—in which no further growth by addition of parts takes place, and exocœlic radii in which such growth does take place, and in the absence of such a division the metacnemial growth processes of the *Edwardsiæ* are not comparable with those of the *Actiniæ*. But a reference to Text-fig. 2, *h*, founded on my recent demonstration of the sequence of micromesenterial and tentacular formation in *Edwardsia carnea* (4), shows a certain parallelism between the growth principle in the two cases, for in *Edwardsia* new mesenteries and new tentacles are formed alternately dorsal and ventrad of the primary megacœlic tentacle x , which

thus assumes a median position in each growth-sextant, and is actually median when the number of tentacles is an uneven number. And, if one keeps in view this principle of the addition of parts alternately dorsad and ventrad of the median tentacle in each sextant, it is possible to construct a scheme showing the derivation of the Actinian from the Edwardsian mode of growth. For if the first-formed micromesentery in a growth-sextant of *Edwardsia*—that on the left in the diagram *h*—were formed as a pair instead of a single and if a tentacle grew out of the endocœle thus established, one would get the same relations of micromesenteries to tentacles as in diagram *a*. And, again, if the micromesentery on the right in diagram *h* were, in succession, to be formed as a pair instead of a single, one would get a stage actually represented in *Phellia*, but not represented in any of the diagrams in the Text-fig. because, as noted above, two or more successive growth stages are represented in each diagram for economy's sake. Such a scheme would be perfectly legitimate for the dorso-lateral megacœles of an *Edwardsia*, and I have accordingly, in diagram *h*, represented the muscle banners of the macromesenteries in the position they would occupy in such a megacœle. But in the lateral and ventro-lateral megacœles the scheme is somewhat vitiated by the necessity of taking into account the macromesenteries *v* and *vi* in order of Actinian development, which, pairing with *ii* and *i*, make up six primary mesenterial pairs of the Actiniæ. The difficulty is not insuperable, for, as I have shown elsewhere, the order of appearance of the micromesenteries is reversed in the ventro-lateral megacœles of *Edwardsia carnea*, and may be reversed in the lateral megacœles in other species, and one has only to suppose that the mesenteries first formed in these sextants become macromesenteries in order to arrive at the paired hexamerous condition. This form of argument, however, is extremely hypothetical, and I do not propose to push it any further. It is sufficient for present purposes if I have succeeded in interpreting the facts of the developmental succession of the

mesenteries and tentacles in Actiniæ as represented by Ilyanthus by reference to the simpler and more primitive succession observed in the Phelliinæ, and if I have further established certain analogies between the growth processes in the Phelliinæ and those in the Edwardsiæ.

It remains to discuss the relationships of the Phelliinæ with other Actiniæ, a task which, in the present state of our zoological knowledge, presents considerable difficulties. Proceeding on the accepted methods of systematic zoology, we may accept, as the definition of the family Sagartiidæ, "Actiniæ provided with acontia," and it follows logically that the Phelliinæ are included in the Sagartiidæ. As to the limits of the Phelliinæ, I think there can be no doubt that the genus Phellia, with Decaphellia and possibly Halcampactis, form a group distinct from the Chondractiniinæ of Haddon, who, in my opinion, has already sufficiently established the validity of the latter family, and a study of sections of *Paraphellia expansa*, Haddon, has satisfied me that there is little in common between this genus, long since included in the Chondractiniinæ, and the Phelliinæ. *Paraphellia* is anatomically very similar to *Sagartia*. As to the nearest affinities of the Phelliinæ, it has been obvious, in the course of this paper, that I regard them as most closely related to the "Actinies pivotantes" of French authors, the Ilyanthidæ of Gosse. But then arises the question as to what forms should be included in this somewhat heterogenous group. Certainly not the Edwardsiæ, for reasons which I have already given (4). Observations that I have made, but not yet completed, on the anatomy of *Ilyanthus mitchellii*, Gosse, indicate that this species is quite distinct from the others commonly grouped with it. I am doubtful of the near relationship of *Siphonactis* to *Halcompa*, and am unable to express an opinion on *Eloactis* as I have not had an opportunity of studying this genus. There remain the genera *Halcompa*, *Halcompella*, and *Halianthella*, which I prefer to group together in a family *Halcompidæ*, notwithstanding the

presence of a mesoglœal sphincter muscle in *Halianthella*, and I agree with Andres in separating these forms from the other "Actinies pivotantes." It is to the *Halcampidæ* that the *Phelliinæ* appear most closely related, rather than to the *Sagartiidæ*, for reasons which I will set out at full length.

The structural and external features which, taken in combination, are the recognisable marks of the members of the *Phelliinæ* are :

(1) The division of the column into capitulum, scapus, and a more or less inflatable but adherent base or physa. (2) The corrugation of the external surface of the scapus, correlated with the presence of a coriaceous investment known as the cuticle or epidermis. (3) The predominant size and importance of the six pairs of primary mesenteries which alone are attached to the actinopharynx. (4) The dwarfed condition of the secondary, tertiary, and, when present, of the other cycles of mesenteries, which are reduced to little more than a lamina supporting the parietal muscles. (5) The relatively considerable development of the parietal musculature, and its symmetrical arrangement on either side of the peripheral edges of the macromesenteries and micromesenteries. (6) The great development and circumscribed character of the longitudinal retractor muscles of the macromesenteries, and the reniform shape of these muscles in section. (7) The capacity for introverting the distal third of the scapus as well as the capitulum, correlated with the great development of the retractor muscles. (8) The reduction to the point of suppression of the longitudinal retractor muscles of the micromesenteries. (9) The fertility of the macromesenteries only. (10) The sterility of the micromesenteries. (11) The presence of a mesoglœal sphincter muscle. (12) The presence of acontia. (13) The reduction of the peristomial musculature, causing the actinostome to gape.

As far as can be judged from the evidence afforded by simple observation, all members of the *Phelliinæ* breed true to these characters; but, as I have shown, every character is subject to considerable variation within the group. A critical

study of these marks or characters shows us that, whilst all of them taken together constitute what we call a *Phellia*, there is hardly one of them that is peculiar to the group, unless it be No. 13. Nos. 9 and 10 are in a large measure peculiar and differential characters, but not wholly so, for, as I have shown, there is probably an infertile couple of macromesenteries in *Phellia castanea*—a feature which approximates this species to *Halcompa*, in which the macromesenterial couples I-III are alone fertile. *Halianthella*, Kwietn., a member of the same family as *Halcompa*, has all the six pairs of macromesenteries fertile and no others, and thus is in exactly the same condition as *Phellia*.

On a further analysis of the characters enumerated above, we find that those which are not differential are distributed sporadically in several groups of Actiniinæ, and occur in different combinations in those groups. Thus, character 1 is found in the Edwardsidæ, Halcompidæ, in *Ilyanthus*, in *Siphonactis*, and in other forms in various degrees of distinctness. Character 2 is shared by the Edwardsidæ and Chondractiniinæ, and by *Aureliania*, Gosse; *Capnea*, Gosse; and *Ammonactis*, Verrill. Characters 3 and 4 reappear in the Halcompidæ, Metridiinæ, Chondractiniinæ, and in *Siphonactis* (I do not include the last-named among the Halcompidæ). Character 5 is found in the Edwardsidæ and Halcompidæ, in *Eloactis*, Andr., and generally in all forms that have very highly developed and circumscribed retractor muscles, but also in some Chondractiniinæ, e. g. *Hormathia*, in which the retractors are diffuse. Characters 6 and 7 are found in Edwardsidæ, Halcompidæ, and *Eloactis*, and among the Chondractiniinæ in *Paraphellia expansa*, which has large circumscribed retractor muscles on the macromesenteries, but, as far as I have been able to observe, no capacity for introverting the upper part of the scapus. Character 8 goes, as a rule, with character 6, but in *Paraphellia expansa*, and generally in the Chondractiniinæ, longitudinal retractor muscles are present on at least the higher orders of micro-mesenteries, whether the retractors of the macromesenteries

be specially developed or not. Characters 9 and 10 are elsewhere found only in the Halcampidæ, including Halianthella in this family. Character 11 is found in all members of the family Sagartiidæ (auctt.) except Aiptasia, but also occurs in the Paractidæ and in Halianthella. Character 12 has hitherto been regarded as diagnostic of Sagartiidæ, but it should not be forgotten that analogous, though not exactly similar, structures are characteristic of the Cerianthidæ.

From this analysis it appears that of the thirteen characters enumerated as marks of the group Phelliinæ, no less than ten, and in part an eleventh, recur in the Halcampidæ (including the Halianthinæ); six recur in the Edwardsidæ; four, and in part a fifth, recur in the Chondractiniinæ, four in the Metridiinæ, and two only in the Sagartiinæ. If we may judge of the relationships of animals, and therefore of their places in a natural classification, by the sum of their characters rather than by one or two somewhat arbitrarily selected, the Phelliinæ certainly incline on the balance towards the Halcampidæ rather than towards any other of the sub-families commonly included in the Sagartiidæ.

The main reasons for including the Phelliinæ in the Sagartiidæ are the presence of acontia and of a mesoglcæal sphincter muscle. But Halcampactis, in all other respects a Halcampid, has acontia, and Halianthella, in all other respects a Halcampid, has a mesoglcæal sphincter muscle.

Are we to regard Halianthella, Halcampactis, and the Phelliinæ as the representatives of a stage in the evolution of Sagartiæ with acontia and a mesoglcæal sphincter muscle from a Halcampa-like ancestor? Assuredly not as representatives of the direct line of descent, for in the first place Halianthella has only one and Halcampactis the other of the required characters; and in the second place the differences between the mesenterial arrangements of the Phelliinæ and the Metridiinæ, Sagartiinæ, Chondractiniinæ, and other groups included in the Sagartiidæ are so great as to be fundamental. Then the two lines, or possibly the several lines represented by the different families, must have diverged at an early

period from a common ancestral stock which had acquired acontia, and is now possibly represented by *Halcampactis*, though *Halcampactis* has not acquired a mesoglœal sphincter, whilst *Halianthella*, which possesses no acontia, has.

Such an argument assumes that the possession of acontia is a mark of close genetic relationship and involves the inclusion of a heterogeneous group of Actinians, among others *Aiptasia*, in the family *Sagartiidæ*, the limits of which have been the subject of much discussion (see Andres (1), Hertwig (19), Kwietniewsky (22), and Haddon (15)). But is it not possible that acontia, which cannot be regarded as anything else than a special modification of the ubiquitous mesenterial filament, may have been independently acquired by several groups of Actinians?

We may test this suggestion by inquiring into the distribution of another character, e. g. the mesoglœal sphincter muscle. This is present in all the Actinians that have acontia except *Aiptasia* and *Halcampactis*. It is also present in *Halianthella*, in *Ophiodiscus*, and in the *Paractidæ*. It is a character which has been held to be of considerable classificatory importance. If so, it should afford some guide to genetic relationships. But when we take the mesoglœal sphincter into consideration along with acontia to what conclusions are we led? If a mesoglœal sphincter is a sign of descent from a common ancestor, then *Halianthella*, *Ophiodiscus*, the *Paractidæ*, and the *Sagartian* sub-families of *Metridiinae*, *Sagartiinae*, *PHELLINEE*, and *Chondractiniinae* are genetically related; the *Aiptasiinae* and *Halcampactis* are not, because they have not got a mesoglœal sphincter. But we have just seen that the *Aiptasiinae* and *Halcampactis* are related to the other sub-families of *Sagartiidæ* because they have acontia, and that *Halianthella*, *Ophiodiscus*, and the *Paractidæ* are not related because they have no acontia. If acontia are taken as the criterion of descent from a common ancestor, then *Aiptasia* and *Halcampactis* must either have independently lost the mesoglœal sphincter or have never acquired it. If the mesoglœal sphincter is taken as a cri-

terion, then the Sagartiidæ and Halcampactis must have acquired acontia independently of the Paractidæ, of Ophidiscus, and of Halianthella; or these latter forms must at some time have possessed acontia and subsequently lost them. Whichever way one looks at it, there is the question of the acquisition of a new character or the dropping out of a character previously existing.

It will be more logical, however, to regard the phenomena from the following standpoint.

There are four possible combinations, viz. :

(1) + Mesogloæal sphincter, + acontia : Metridiinae; Sagartiinae; Phelliinae; Chondractiinae.

(2) + Mesogloæal sphincter, - acontia : Halianthella; Paractidæ.

(3) - Mesogloæal sphincter, + acontia : Halcampactis; Aiptasia.

(4) - Mesogloæal sphincter, - acontia : Actinia, Anemonia, Bunodes, etc.

(The plus and minus signs stand for presence or absence of the character in question.)

It will be observed that every possible combination is represented and that some of the combinations bring together forms between which no relationship has even been suggested, e. g. Halianthella and the Paractidæ.

We may go a step further and bring in another element, choosing the predominant size and "perfection" of the primary mesenteries only. Then, if we denote the presence of a mesogloæal sphincter by M., the presence of acontia by A., and the perfection of only the first cycle of mesenteries by I., and use the plus and minus signs as before, we get eight possible combinations, viz. :

(1) + M. + A. + I. : Metridiinae; Chondractiniinae, Phelliinae.

(2) + M. + A. - I. : Sagartiinae.

(3) + M. - A. + I. : Halianthella.

(4) + M. - A. - I. : Paractidæ.

(5) - M. + A. + I. : Halcampactis.

(6) — M. + A. — I. : Aiptasia.

(7) — M. — A. + I. : Halcompa.

(8) — M. — A. = I. : Actinia, Anemonia, Bunodes, etc.

Again, all the possible combinations are represented by described forms of living Actinians. This method of presenting the facts might be carried further by successively introducing new elements, but it would quickly become so complicated as to require mathematical treatment, and I do not propose to pursue the subject in this place.¹

What I want to emphasise is that we are dealing with unit characters, each of which may be present or absent, and when present may enter into all possible combinations with the other unit characters. In brief, these unit characters have all the properties of, and may legitimately be identified with Mendelian units.

This being the case is it not probable, and more than probable, that among the many "factors" that go to make up the full complement of variable Actinian characters there are some which, when brought together in the germ-cell, lead to the production of that particular outgrowth called an acontium? And if this be the case, does it not follow from the evidence accumulated by the experiments of the last fifteen years, that in any given Actinian germ-cell there may be some of the factors necessary for the production of an acontium, but that they will not lead to the exhibition of that feature in the adult organism unless one or more additional factors are added to them? I submit that the Phelliinæ give considerable support to this view, for in them the acontia show every possible grade between full development and reduction to the point of disappearance, and the most reasonable explanation of this phenomenon is that in some species

¹ The number of possible combinations is 2^a , where a stands for the number of unit characters entering into combination. Thus the addition of a fourth element would give sixteen possible combinations, and if all the twelve elements enumerated above as characters of Phelliinæ but also occurring in other groups of Actinians were taken into account the possible number of combinations would be 2^{12} or 4096.

(or varieties) there is missing a factor required for the full development of the structures in question.

If this be a true explanation, and it is the most consistent with recent researches, we can account for the appearance or disappearance of acontia in groups having very different combinations of other characters, and we get rid, once and for all, of the idea that the presence of this single character is such a positive mark of inter-relationship that all the forms possessing it must be united into a single family. The same reasoning applies to the mesogloæal sphincter and to every other structural feature which can be shown by the methods indicated above to be independently variable. I may claim also that this method of dealing with observational data throws a new light on the phenomena of homoplasy or parallel development, which I have dealt with on previous occasions in connection with other animals. Applying these principles to the subject in hand, it is obvious that the group Sagartiidæ, including Halcampactis, the Aiptasiinæ, the Metridiinæ, the Sagartiinæ, the Phelliinæ, and the Chondractiniinæ must be broken up. Halcampactis, judged by the sum of its characters, takes its place with the Halcampidæ. On the same principle, Aiptasia goes alongside of its obvious ally, Anemonia. The Phelliinæ, as I have shown, must stand apart from the other sub-families, and be approximated to the Halcampidæ. Of the remaining groups the Metridiinæ will be found to share one set of characters with the Chondractiniinæ, another set with the Sagartiinæ, and further analysis may lead to further subdivisions. It is also evident that the same principles will have to be applied to the whole of the Actiniinæ; but I am not in a position, and do not propose, to make such an ambitious attempt now.

If the method of dealing with systematic questions which I have recommended and briefly indicated in the foregoing paragraphs were accepted and generally adopted, it would have a result, unpalatable to many zoologists, of undermining many accepted beliefs on phylogenetic questions. But this, I beg leave to submit, would be wholly advantageous to the

progress of zoology. It is not possible to read Tower's investigations on the evolution of the genus *Leptinotarsia* and Morgan's critique of the 'Theory of Evolution,' together with much other current Mendelian literature, without experiencing grave doubts as to the validity of a large part of current, systematic, and phylogenetic speculations. All this class of reasoning is open to the fundamental objection taken against it by Morgan, that we collect a large number of "characters," external or anatomical, and arrange them in a series which we call evolutionary, without having any evidence as to the actual relationship by way of descent and inheritance among the different forms constituting our series. On the other hand, breeding experiments show direct genetic relationship between forms that one would never have supposed to have descended one from the other, and contrariwise, more remote relationship between forms which, on accepted methods of systematic criticism, one would unhesitatingly have placed in direct lines of descent. "Çela donne," or, at any rate, doit donner "furieusement à penser."

Having for some years past recognised the force of such criticisms as those mentioned in the preceding paragraph, and being convinced of the importance of bringing morphological and systematic studies into harmony with the principles established by genetic researches, I have endeavoured in the foregoing pages to arrange certain limited morphological and systematic data in conformity with the conclusions reached by the Mendelian school of zoologists, and have indicated a method that seems to me appropriate to the purpose. In so doing I am aware that I am proposing a revolution in our methods of envisaging and dealing with morphological and systematic problems, and have only given the barest outline of the plan which I propose to pursue. It is possible, as I perceive from some attempts that I have made in the course of writing these few pages, to carry the ideas I have propounded much further, and to give much greater precision to the methods roughly sketched out above. But the subject is one of great size and complexity, and therefore inappropriate

to the concluding passages of a memoir undertaken with only a limited object in view. My suggestions are, therefore, given for what they are worth in their present state of incompleteness, and a further discussion of the possibility of co-ordinating morphological, systematic, and genetic data must be postponed to a future occasion.

LIST OF THE PRINCIPAL PAPERS REFERRED TO IN THE TEXT.

1. Andres, A.—“Actinien.” ‘Fauna und Flora des Golfes von Neapel,’ ix, 1884.
2. Beneden, E. van.—“Die Anthozoen der Plankton Expedition.” ‘Ergeb. der Plankton Expedition d. Humboldt Stiftung,’ Bd. ii. K. e.
3. Bourne, G. C.—“Report on the Solitary Corals collected by Prof. Herdman at Ceylon,” ‘Ceylon Pearl Oyster Fisheries,’ Supplementary Report, xxix, Published by the Royal Society, 1905.
4. ——— “A Description of Five New Species of *Edwardsia*, Quartr., from New Guinea,” ‘Linn. Soc. Journ.,’ xxxii, 1916.
5. Carlgren, O.—“Studien über nordische Actinien,” ‘Kongl. Sven. Vet-Akad. Handl.,’ xxv, 1893.
6. Carlgren, O.—“Zoantharien,” ‘Hamburger Magalhaenische Sammelreise,’ Hamburg, 1898.
7. ——— “Actiniarien d. Olga Exped. Wissensch. Meeresuntersuchungen,” v.
8. Dixon, F.—“On the Arrangement of the Mesenteries in the Genus *Sagartia*, Gosse,” ‘Proc. Roy. Dublin Soc.,’ New Ser., vi, 1888.
9. Dixon, G. Y.—“Remarks on *Sagartia venusta* and *Sagartia nivea*,” *ibid.*, New Ser., vi, 1888.
10. ——— and Dixon, F.—“Notes on *Bunodes thallia*, *Bunodes verrucosa*, and *Sealia crassicornis*,” *ibid.*, New Ser., vi, 1889.
11. Duerden, J. E.—‘The Coral *Siderastræa radians* and its Post-larval Development,’ Washington, 1904.
12. Farquhar, H.—“Preliminary Account of Some New Zealand Actinaria,” ‘Linn. Soc. Journ.,’ xxvi, 1898.
13. Faurot, L.—“Études sur les Actinies,” ‘Arch de Zool. expér. et gén.’ (3), ii, 1895.